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ON THE NATURE OF THE STIMULUS WHICH CAUSES THE CHANGE OF FORM IN POLYMORPHIC GREEN ALGÆ.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XXII.

(WITH PLATES XVII AND XVIII)

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Introductory.

ALTHOUGH the work of Klebs and others[1] has demonstrated clearly that there exist a number of polymorphic species among the green algæ, yet up to the present time the exact nature of the stimulus which brings about the change in the manner of growth has not been determined. To throw some light upon this question the experiments to be described in the present paper were begun. They were carried on in part at the Botanical Laboratory of the University of Michigan, during the spring and summer of 1898, and in greater part at the Hull Botanical Laboratory of the University of Chicago, during the year just past.

[1] FAMINTZIN, A.: Die anorganische Salze als Hilfsmittel zum Studium der Entwickelung niederer chlorophyllhaltigen Organismen. Mélanges biol. St. Petersbourg **8**: 225. 1871.

CIENKOWSKY, L.: 1. Zur Morphologie der Ulothricheen. Mélanges biol. St. Petersbourg **9**: 531. 1876.

———: 2. Ueber Palmellenzustand bei Stigeoclonium. Bot. Zeit. **34**: 17. 1876.

GAY, F.: Recherches sur le développement et la classification de quelques algues vertes. Paris, 1891.

KLEBS, G.: Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. Jena, 1896.

Descriptive.

A species of Stigeoclonium (perhaps a form of *S. tenue*), found growing with Pleurococcus, etc., on moist bark at Ann Arbor, was chosen for experimentation. It shows two very distinct and easily distinguishable forms according to the culture medium in which it is grown. The normal form is that of Palmella. A culture of this form shows the surface of the fluid covered with spherical cells 12 to 15 μ in diameter. The cells multiply by division in planes generally vertical and at right angles to each other, and the daughter cells separate more or less completely after division is accomplished (*figs. 1, 6, 12, 27*). The walls are quite thick and somewhat gelatinous on the exterior, though not by any means so markedly as in the form studied by Cienkowsky (*l. c.*, *2*), and the protoplasm is quite coarsely granular. The chloroplast has the form of a hollow spherical shell with an opening in one side, which has a diameter about equal to the sphere's radius, varying somewhat in different cells. Sometimes the opening is nearly a great circle of the sphere (*fig. 1, a, b*). This opening in the chloroplast is probably the "bright spot" described by Cienkowsky. There is always a pyrenoid present in each cell, and sometimes two are found. This body has a diameter of about 3 μ, and lies in a thickened region in the chloroplast. When the cell is about to divide the chloroplast separates into two parts, each part taking a half of the original pyrenoid, and a wall forms between the two portions (*fig. 1, c*). The plane of division always intersects the plane of the opening in the chloroplast. Then the two hemispherical cells become more and more spherical, splitting the wall between them along its middle lamella, until finally, if nothing prevents, they come to lie as two separate spheres side by side (*fig. 1, a*). Very often division proceeds more rapidly than this rounding off, and there results a group of four or more cells making contact with each other in plane surfaces (*fig. 6*). Often this process is continued without any parting till there results a plate of cells spread out over the surface of the nutrient medium. Sometimes, too, the planes of division lie parallel to the surface of the

medium as well as perpendicular to it, and a parenchyma-like mass of polygonal cells is formed, projecting down into the fluid and up into the air (*figs. 6, 24*). After division the chloroplast enlarges until it occupies about as much of the daughter cell as the mother chloroplast did of the mother cell. The form just described will be termed throughout this paper the *palmella form*.

In the other form we have a very different mode of growth. The cells are not spherical, but cylindrical; they divide, excepting at the origin of a branch, only by transverse planes, and show no tendency to break apart, but remain closely connected to form branching filaments (*figs. 2, 8, 18*). This will be termed in the following discussion the *filamentous form*. The cells of the filaments are 4.5 to 10μ in diameter and from two to four times as long. The longest filaments are 175 to 200μ long and their branches extend in all directions. No true hairs have been seen, but often the tips of the filaments are very narrow. The protoplasm is not granular, as in the palmella form, but usually contains two to seven refractive bodies smaller than the pyrenoid, but looking much like it. They are probably of an oily nature. They have a diameter of about 15μ, that of the pyrenoid being, as in the other form, about 3μ. The chloroplast is elongated to suit the cell and becomes somewhat trough-shaped; lying along one side of the cylindrical wall it reaches about one half way around the cell and usually partially covers one end, sometimes both. Its opening is thus longer than in the other form. The pyrenoid lies somewhere in a thickened part of the chloroplast.

Reproduction in both forms is accomplished by comparatively large asexual biciliate zoospores. These are the microzoospores of Klebs. I have observed no conjugating zoospores. The chloroplast of the mother cell divides into four to eight parts along curiously parallel planes running nearly at right angles to the plane of the opening (*fig. 1*). Each of these portions, with its share of the protoplasm, becomes a zoospore. After division is complete and the zoospores are nearly formed, the daughter

chloroplasts often lose much of their bright green color and become pale. Palmelloid cells usually produce seven or eight zoospores; the number produced by a filament cell depends upon its size. The zoospores are ellipsoidal to spherical when discharged into the water by the rupture of the parent wall, and immediately begin to move about, swimming by means of two long cilia (*fig. 3*). Each contains a pyrenoid, and often several smaller granules; the chloroplast can be seen lying against the wall opposite the origin of the cilia and extending in its usual cup-shaped form somewhat more than half way around the cell. The dimensions of motile zoospores are from $3\times6\mu$ to $6\times9\mu$. After swimming freely for several hours, the motion of the cilia becomes sluggish and finally ceases altogether; the zoospore comes to rest and assumes the spherical form. The diameter is now not far from 6μ. The chloroplast then regains its original bright color, the cell enlarges, and, if conditions are favorable, may go over imperceptibly into the palmella form. The cell thus produced may divide a number of times, as described above, and then produce more zoospores; or it may produce them immediately upon the attainment of its full size, or even earlier; or it may become a resting cell and remain quiescent indefinitely.[2] However, a zoospore does not usually show this mode of growth. It generally elongates as it lies on the surface (or sometimes at the bottom) of the fluid, and becomes a cylinder with rounded ends. As it grows longer it bends so that it becomes somewhat crescent-shaped, semicircular, or even horseshoe shaped, and soon divides into two cells by a transverse wall near its middle (*figs. 8, 32*). Thus a filament is started, which soon branches. Its cells produce zoospores sooner or later, according to conditions.

Methods.

Pure cultures were first obtained by growing in nutrient solution in suspended drops; then the material was transferred to

[2] KLEBS, G.: Loc. cit.

PRINGSHEIM, N.: Ueber die Dauerschwärmer des Wassernetzes. Monatssch. d. Berliner Akad. 1860.

small, loosely covered glass dishes containing from 5^{cc} to 10^{cc} of solution. The cultures stood on glass shelves close against the panes of an east or west window, and were always shaded from the direct rays of the sun by a curtain of white muslin, which was left constantly in position during the high temperatures of the summer months. Examination of cultures was made from time to time by transferring the dish with its contents directly to the stage of the microscope and using an objective of medium low power.

The culture media used were modifications of the well-known fluid of Knop,[3] consisting of the following salts: calcium nitrate, four parts; magnesium sulfate, one part; potassium nitrate, one part; di-potassium acid phosphate, one part; iron, a trace. Owing to the extreme weakness of the solutions to be used, it was deemed advisable to secure at the outset, as nearly as might be, the exact proportions of the constituent salts here given, and to this end the following method was adopted. By reference to tables of the physical properties of solutions,[4] the corresponding specific gravity and gram-molecular strength of solutions of the first three of the above salts were found. By the use of these data a stock solution of each of these compounds was made up, so that it contained a specific number of gram-molecules per liter. The specific gravity bottle was used in these determinations, and temperature was always taken into account. For the fourth salt in the list data could not be found; therefore it was formed in solution from normal solutions of phosphoric acid and potassium hydroxid. The physical constants for these could be found. The accuracy of this method for producing K_2HPO_4 was tested by volumetric analysis and found to be satisfactory. The specific gravity of a normal solution of this salt so made was found to be 1.13207 at 15° C. Redistilled water was used throughout all of the work.

The stock solutions thus prepared were kept in flasks tightly stoppered with rubber; their specific gravity was taken from

[3] KLEBS, G.: op. cit., p. 8.

[4] E. g., those given by WHETHAM, W.C.D., Solution and Electrolysis, 215. Cambridge. 1895.

time to time, and water was added as it was lost by evaporation. Knowing the gram-molecular, and hence the percentage, strength of these stock solutions, any strength of Knop's solution may readily be made up from them; and solutions so made up are much more accurate in their proportions than those made in the ordinary way; for in dealing with salts such as magnesium sulfate and calcium nitrate the amount of water contained in the compound as taken from the laboratory bottle is always an uncertain quantity. All troubles arising from crystalline and amorphous, as well as deliquescing, salts may thus be readily avoided. The exact amount of ferric salts in my solution was not determined. The transfers of material from an old culture to a new were made, after a pure culture was obtained, by means of a needle. This was first heated in a flame and then cooled by plunging in the new culture fluid. Bits of steel always scaled off in this operation, and these furnished sufficient iron for the plants.

In making up culture media from the stock solutions of the constituent salts, it is necessary to dilute as far as possible before bringing the K_2HPO_4 and $Ca(NO_3)_2$ together. As was remarked by Klebs, this avoids, in a great measure, the separating out of quantities of $CaHPO_4$. This method is not completely satisfactory, however, and it would be better so to modify the proportions as to avoid the white precipitate entirely. I have planned to do this in future work. A solution made up of the quantities of the salts given by Knop dissolved in 93 parts of water is, of course, a 7 per cent. solution (since the iron is of such small amount it may be disregarded). This was further diluted to 1 per cent., 1.5 per cent., and 2 per cent. for growing the stock material.

Investigation.

At the outset it was found that if material in the palmella form were transferred from a 1 per cent., 1.5 per cent, or 2 per cent. solution where it had been growing for some time, to a solution of less than 0.5 per cent., the plants responded to the

change in solution strength, and sent out long filaments from the original palmella masses (*figs. 7, 15, 16*). Also the palmella cells produced numerous zoospores. These germinated, as previously described, to produce, not the parent form, but the widely different filamentous one. Conversely, it was found that if filaments, produced as above, and growing healthily in a 0.2 per cent. or 0.25 per cent. nutrient solution, were changed to one of 1 per cent., 1.5 per cent., or 2 per cent. strength, the response was scarcely less well marked than in the other case; the cells of the filaments soon became spherical, and changed to the palmella form by dividing in both longitudinal and transverse planes (*figs. 4, 5*). In the strong solutions few or no zoospores were produced. Where a few were produced they changed, either directly or after the first or second division, to the palmella form.

With these two facts in view the attempt was made to determine where, in this change of solution strength, lies the necessary stimulus for the production of the corresponding change of form. A stimulus arising from a change of solution strength (always retaining the same salts in the same proportion) may be of any one of three different natures. (1) It may be of a chemical nature: *i. e.*, it may be due to a change in the amount of salts with which the organism is supplied. This implies three possibilities: (*a*) the plant may be affected by the increase or decrease in all the inorganic salts. (*b*) Again when such change is made it may be the change in amount of a single salt, say potassium nitrate, to which the plant responds. There are four possibilities under this head, one for each of the four salts used. (*c*) Again, it may be possible that neither of the preceding suppositions is true, but that the response is due, not to all the changes together, nor to any one alone, but to a combination of two or three of them. For example, it may be a change in the amount of potassium phosphate together with that of calcium nitrate, which acts as a stimulus. We know that, excepting in very weak solutions, these two salts react chemically upon each other, so that it is at least conceivable that an

increase or decrease in both of them together might influence the plant differently from a corresponding change in only one. Under this head there are no less than ten possibilities, six taking the salts by twos, and four by threes. (2) Further, the stimulus may be of a physical nature and due, not to the change of salts at all, but to a change of osmotic pressure upon the living cell. This osmotic change may be effective in several ways. (*a*) It may be that the response is due to a change in the osmotic pressure of the solution in *general*. When the saline constituents of the solution are increased or decreased as a whole there is a corresponding change in the so-called osmotic strength. (*b*) However, it may be, as suggested by Copeland's recent work,[5] that the plant is more influenced by osmotic pressure when this is derived from one salt than by the same pressure derived from another. And if this be the case, then this influence is as complicated a one as that of the change in the conditions enumerated under (1) above. (3) Finally, the response in the plant may be due both to the stimuli from chemical composition and to those from osmotic pressure, a combination of (1) and (2) above.

My experiments were devised to determine primarily whether the stimulus is a chemical or a physical one. For this it is necessary to have solutions in which the relative and absolute amounts of saline constituents can be varied without changing the osmotic pressure of the salt content as a whole, and this must be brought about, as far as may be, without the introduction of any new conditions. It is necessary first to know the osmotic pressure of the complete Knop's solution. Now the pressure of any weak solution of several constituents is equal, at least approximately, to the sum of the partial pressures of the constituent salts, as these pressures would exist if the salts were separately put into a simple solution whose volume equaled that of the complex one. This principle makes it a simple matter to calculate the pressure of complex solutions of

[5] COPELAND, E. B.: The relation of nutrient salts to turgor. BOT. GAZ. **24**: 399. 1897.

non-electrolytes. But the pressure of a simple solution of an electrolyte is not so easily calculated. On account of dissociation, such pressure is much greater than that of a solution of a non-electrolyte of the same gram-molecular concentration. It was this fact with which DeVries[6] was dealing when he derived his so-called isotonic coefficients. But since his range of concentration was very limited, he was unable to get at the truth of the matter; and the result is, that, though his coefficients may be, and doubtless are, true for a certain strength of solution, yet, since dissociation itself varies with the concentration, they are not true in general. However, in weak solutions dissociation becomes nearly complete, and if we assume that it is complete we shall probably be able to approach the truth much more nearly than by following the method of DeVries. My solutions are all very weak, and I have no doubt that my approximations by this method are, as a rule, quite nearly true. By assuming complete dissociation, the calculated osmotic pressure for any solution becomes that of an equimolecular solution of a non-electrolyte, multiplied by the number of ions derived from a molecule of the salt under consideration. This makes the calculation very simple. Taking the pressure of one gram-molecule per liter of some undissociated substance as a unit, *N*, table I gives the partial pressures of the complete solution which was used as standard. This is practically the same as a so-called 2 per cent. Knop's solution as usually made up. In the pressure columns, *a* is derived by assuming ionization complete; *b* by DeVries' method; and *c* gives the actual pressures for those salts for which data of dissociation could be found. The discrepancy between *a* and *b* lies almost wholly in the $Ca(NO_3)_2$. Here we should make a greater error in using DeVries' coefficients than in assuming complete dissociation. Column *n* gives the number of ions derived from a molecule, *i* is the ratio between the actual osmotic pressure and that of an equimolecular solution of a

[6] DeVries, Hugo: Jahrbücher für wiss. Bot. **14**: 427. 1884.
Donders and Hamburger: Zeit. f. Physikal. Chemie **6**: 319. 1890.

non-electrolyte. N at 0°C., is 1686 cm of mercury, or 22.18 atmospheres.

TABLE I.

Salt	Gram-molecule per liter	n	Partial pressures in terms of N			
			a	b	c	i
$Ca(NO_3)_2$ - -	.07143	3	.21429	.28571	.175004	2.45
KNO_3 - - -	.02857	2	.05714	.08571	.055712	1.9
$MgSO_4$ - - -	.02381	2	.04762	.04762	.035712	1.5
K_2HPO_4 - -	.01664	4	.06655	.06736	.....	....
Total pressure - - - -			.38559	.48641		

This 2 per cent. strength is the most concentrated solution I have used. Anything stronger kills the alga almost immediately. As we decrease the concentration below this standard 2 per cent. strength the dissociation becomes more and more complete. Thus as the concentration approaches zero as a limit the value of i approaches that of n. The value of i for the different concentrations used, as far as they can be calculated from the physical data at hand, are given in table II. Values for H_3HPO_4 are inserted for comparison, in place of those for K_2HPO_4. Table II also shows the total pressures of the various percentages in terms of N. The pressures in column a will be used throughout this paper, but instead of 0.3856 N I shall write 3856 $N \times 10^{-4}$, etc.

TABLE II.

Total pressures in terms of N.		"Per cent."	Values of i calculated from conductivity data				
a[7]	b		$Ca(NO_3)_2$	KNO_3	$MgSO_4$	K_2HPO_4	H_3PO_4
.38559	.486405	2	2.45	1.9	1.50	....	2.04
.289193	.364804	1.5	2.5 (?)	....	1.56	....	....
.192795	.243203	1	2.55	....	....	....	3.02
.096398	.121601	.5	2.66	1.92	....	....	....
.048199	.060801	.25	2.75(?)	....	1.68	....	....
.019279	.024320	.1	2.9	....	1.83	....	....
.00964	.013160	.05	3	2	1.89	....	4

[7] The meaning of a and b is the same as in table I.

Having shown thus the partial and total pressures of the normal solution, I shall now describe the modifications of this solution which I have used. Four solutions were made up according to the formula given above, excepting that each was deficient in one of the four constituent salts. All of one salt, it was thought, should not be omitted, since then, as in higher plants, pathological responses would probably ensue. In these solutions the deficient salt was reduced to one tenth its normal quantity. The decrease in osmotic pressure, caused in each instance by this diminution of one salt, was calculated by the two methods just spoken of, and of each of the three other salts a sufficiency was added to increase the pressure by an amount equal to one third of the calculated decrease. Two full sets of these solutions were made up and used, one by assuming dissociation complete, the other by De Vries' method. These two solutions were identical in their effects upon the plant. Thus finally we have four solutions in each of which a deficiency of one salt is obtained, and the osmotic pressure of the solution is kept up to normal by an increase in the amounts of the other three salts. These amounts are not equally increased by weight, but according to the pressure which they produce when in solution. I shall designate these solutions as follows: A, deficient in $Ca(NO_3)_2$; B, deficient in KNO_3; C, deficient in $MgSO_4$; D, deficient in K_2HPO_4. K will denote the normal solution as given by Knop. The pressure will be expressed in terms of *N*.

The greater part of my work was done in a comparison of the effects upon the plants of the four solutions just described with the normal one of Knop. They were all diluted, for use in the cultures, to the various strengths given in table II. Also a number of tests were made with solutions of a single salt, using the four salts with which we have been dealing. These simple solutions were made up so as to have the same osmotic pressure as the complex ones just described. They will be designated as follows: E, a solution of $Ca(NO_3)_2$; F, of KNO_3; G, of $MgSO_4$; H, of K_2HPO_4. Calculations for these were made only by De Vries' coefficients.

In all, 278 cultures were made and record kept of each for five to fifty days. They were made at all seasons of the year and in two different years separated by a period of nine months, during which the material was kept alive and changes made from time to time but no records kept. It will be seen that there are two possibly very different questions to be answered in the problem before us. First, what are the conditions that bring about a change from the palmella form to the filamentous form; second, what are the conditions that bring about the reverse change? I shall divide the experimental data which are to follow into two groups corresponding to these two questions. Details of typical responses are given in the explanation of plates.

A. RESPONSES OF THE PALMELLA FORM.

In table III are given the results of fifty-five transfers of palmelloid cells into the different solutions. For convenience, all cultures having the same osmotic pressure are brought together. In the left hand column the letters denote the chemical content of the fluid, as just described. The number of cultures made is given in the second column. In the third is recorded the number of cultures in which the cells multiplied but remained of the palmella form after twenty to twenty-five days. Columns four and five (*Filaments*) give the number in which filamentous branches were produced from the original masses in five to twenty-five days. Those in column four produced few filaments, but continued mostly as palmella; those in column five produced many filaments. In columns six and seven (*Zoospores*) are the numbers which produced few or many zoospores within fifteen to twenty days. Column eight contains those which produced no zoospores for twenty-five days or more. The last two columns record cultures on which definite observatians are lacking, the first with regard to the production of zoospores, the second with regard to the production of filaments at the edges.

TABLE III.

Pressure 96 $N \times 10^{-4}$ or 16.19 cm. Hg.

Solution	Cultures	Palmella	Filam'ts		Zoospores				Filaments ?
			Few	Many	Many	Few	None	Doubtful	
K	12	1	2	4	10	2	..	..	5
A	5	..	1	4	5	..	..	..	..
B	5	..	2	3	3	2	..	..	..
C	5	..	..	5	5	..	..	..	..
D	5	2	..	3	5	..	..	..	..
E	8	..	2	3	7	1	..	..	3
F	2	..	2	..	2	..	..	..	..
G	2	..	1	1	2	..	..	..	..
H	2	..	1	1	2	..	..	..	..

Pressure 193 $N \times 10^{-4}$ or 32.37 cm. Hg.

K	2	..	1	1	..	1	..	1	..
A	2	..	1	1	..	1	1	..	..
B	2	..	2	..	..	2	..	..	..
C	2	..	2	..	..	..	2	..	..
D	2	2	..	..	..	2	..	..	..

Pressure 482 $N \times 10^{-4}$ or 81.27 cm. Hg.

K	2	..	..	..	2	..	..	..	2

Pressure 964 $N \times 10^{-4}$ or 161.86 cm. Hg.

K	7	2	1	3	5	1	..	1	1
A	5	..	3	2	2	1	2	..	..
B	5	2	..	3	5	..	..	..	..
C	5	1	1	3	2	1	2	..	..
D	5	3	1	1	3	..	2	..	..
E	2	2	..	..	..	..	2	..	..
F	2	1	..	1	..	1	1	..	..
G	2	..	..	..	..	..	2	..	1

Pressure 1928 $N \times 10^{-4}$ or 323.71 cm. Hg.

Solution	Cultures	Palmella	Filam'ts		Zoospores			
			Few	Many	Many	Few	None	Doubtful
K	5	3	..	2	2	1	2	..
A	4	1	3	..	..	..	4	..
B	4	2	..	2	..	..	4	..
C	4	..	2	2	..	2	2	..
D	4	2	2	..	1	..	3	..

Pressure 2892 $N \times 10^{-4}$ or 487.59 cm. Hg.

K	5	2	3	..	..	..	5	..
A	5	..	3	2	..	..	5	..
B	5	1	4	..	..	..	5	..
C	5	..	5	..	..	1	4	..
D	5	3	2	..	..	..	5	..
E	2	2	..	..	..	..	2	..
F	2	1	1	..	..	..	2	..
G	2	2	..	..	..	..	2	..
H	2	2	..	..	..	..	2	..

Pressure 3856 $N \times 10^{-4}$ or 647.42 cm. Hg.

K	2	2	..	..	..	.	2	..
A	2	1	..	1	..	..	2	..
B	2	..	2	..	..	..	2	..
C	2	..	2	..	..	..	2	..
D	2	2	..	..	..	..	2	..

General Remarks on Table III.

The plant lived indefinitely in solutions K, A, B, C, and D, of all concentrations, and also in the lower concentrations of E, F, G, and H. But the higher pressures, when caused by the single salts, usually resulted in more or less speedy death. With a pressure of 2892 $N \times 10^{-4}$, it was quite a common thing to find the cells dead within a week. Sometimes they were perceptibly

plasmolyzed before death ensued, sometimes not. Of the four simple solutions one appeared to affect the plant as much as another. The table shows the general result of the experiments almost graphically. In the higher concentrations the larger numbers appear mainly in the middle of the series, in the columns headed *Many*, while the third and eighth columns are nearly vacant. Passing to higher concentrations this gradually changes, until, in the highest, the reverse is true. The following conclusions may be drawn from these data.

1. *Nature of the stimulus.*—The effect of a solution of any given osmotic pressure upon the plant is both qualitatively and quantitatively the same, no matter what the chemical nature of the solution may be. If this effect were due to change in the amount of any one salt, then this fact would have appeared in the course of the experimentation, for my various solutions were devised to test this point. So we have eliminated, as far as the palmella form is concerned, the possibilities designated under 1, *a*, *b*, *c*, and 2, *b*, page 295. The stimulus cannot be of a chemical nature, nor can it be physical and depend more upon the presence of one salt than upon another. Also, we have eliminated 3 from among the possible primary stimuli. Considering the facts shown, it is impossible that the external stimulus should be either physical, with the necessary accompaniment of certain chemical factors, or yet chemical, with the necessary accompaniment of certain physical ones. It is, however, not only possible but probable that the external and primary physical stimulus may cause an internal and secondary chemical one. But that lies beyond the scope of the present research. Thus we are driven to accept 2, *a* as the truth in the matter, and to conclude that the response of the organism is determined by a physical, and never, as far as my experiments have gone, by a chemical stimulus. The effect of osmotic pressure upon the palmella form is a double one. I shall consider, first, the effect upon vegetative growth, and second, that upon reproduction.

2. *Response in vegetative growth.*—In my least concentrated solution (pressure $96\,N \times 10^{-4}$) the mode of cell division almost

invariably changed. In forty-six cultures only three are exceptions to this. The cells at the edge of the original mass elongate and become ellipsoidal or even cylindrical, and when division occurs it is by means of a wall lying transverse to the long axis of the cell (*figs. 7, 15, 16*). Thus filaments grow out around the periphery of the original group. The interior cells do not change their form and do not divide further; at length they form the center of a mass of long radiating filaments. Branching of a cell occurs by means of a papilla-like lateral outgrowth, which is cut off by a wall transverse to its long axis. The walls between the filament cells thus formed do not split; thus there is no bulging of the end walls and no separating of the cells. The older cells of a filament (for division occurs only at the tip) bulge at the sides and become barrel-shaped, but the end walls hold them fast together and prevent them forming true spheres (*fig. 25*). It is apparently this coherence of the walls and the orientation of the walls with reference to the form of the cell which constitutes the filamentous habit.

As the osmotic pressure of the fluid is increased there is a continual lessening tendency on the part of the plant to produce filaments, and there arise fewer and fewer filaments at the edge of the cluster. Also these filaments tend to go back, by a rounding and breaking apart of their cells, into the original form. The older cells of the filaments do this, while the younger ones continue to advance by cylindrical cells (*figs. 4, 5, 10, 25, 31, 34*). In my most concentrated solution (pressure $3856\,N \times 10^{-4}$) there were still five cultures out of ten wherein filaments were formed, but in all but one of these the filaments were only two or three cells in length. Back of these cells a thick strand of palmelloid cells marked the path of the advancing filament tip (*figs. 20, 30*). This change of the cylindrical cell to a spherical one, accompanied, as it is, by a corresponding change in the direction of new walls, will be discussed when we consider the responses in filaments. For the present it is enough to note that with increasing pressure the tendency to produce peripheral filaments decreases, both in the number and in the length they attain

before reverting to the palmella form. In my weakest solution they often attained a length of twenty-five to thirty cells (but the older cells here are destroyed in the act of producing zoospores, which will presently be discussed), while in my strongest solution the few filaments produced seldom attained a length of over two cells. The tips of filaments are quite sharply pointed in weak solutions, but blunt in strong ones.

A maximum pressure beyond which filament growth cannot take place lies somewhere between $1928N \times 10^{-4}$ and $2892N \times 10^{-4}$. No limit was found beyond which no filaments at all could be formed.

3. *Response in reproduction.*—The most marked response of this form to the change in osmotic pressure conditions is the sudden production of enormous numbers of zoospores. In some of my cultures almost every original cell has thus emptied out its contents within ten or twelve days of the date of transference. In general, within a fortnight and often within five days these very weak solutions become literally swarming with zoospores, and their production continues as long as the pressure remains low. Zoospores come both from original spherical or parenchyma-like cells and from the older cells of filaments radiating from the palmella mass. This method of producing zoospores has often been resorted to by various writers, and Klebs especially has found it successful in a great variety of forms. But, as far as I know, previous writers have not tried to determine the real nature of this weak solution stimulus.

As would be expected from the response in vegetative growth, when zoospores come to rest in these weak solutions and begin to enlarge, they do so by elongating into a cylinder, which soon divides transversely and later produces branches (*figs. 8, 14, 18, 32*). Thus the response to low osmotic pressure of a zoospore which has come to rest is the same as that of a young cell of the palmella form. Zoospores often grow at both ends, however, which I have not observed in case of other cells. The two cells formed by the first division of the zoospores thus sometimes become a base from which reach out two long branching filaments (*figs. 2, 18*).

In solutions of greater pressure zoospores are produced more and more tardily and in fewer and fewer numbers. The limit to the healthy production of zoospores lies at a pressure of about 964 $N \times 10^{-4}$. Their production in a higher pressure is exceptional and I have never seen them produced at all in my strongest solution. With a pressure of 964 $N \times 10^{-4}$ all zoospores germinate very soon in the manner already described; some of them go directly into the palmella form while most of them germinate to produce filaments of two to five cells, and then these pass into the palmella condition by rounding and breaking up (*figs. 17, 19*). Thus it often comes about that cultures with this pressure show both forms growing together, short young filaments and free round cells as well as parenchyma-like masses. With pressures above the observed limit the spores, when they are produced, usually grow directly into the palmella form, and then continue to grow slowly, or go into the resting stage. I have given little attention to the fate of these resting spores. They retain their green color and remain indefinitely at the bottom of the culture dish. Klebs has described these and states that they may be made to germinate after complete drying out.

B. RESPONSES OF THE FILAMENTOUS FORM.

Experimental data from 169 transfers of filaments into the various solutions are presented in table IV, which is constructed on the same plan as table III. Whether or not the original material changed into the palmella form is shown in the third, fourth, and fifth columns. Cultures in which all or nearly all the cells went over into the other form within a period of thirty days are recorded in the third column; those in which some, but not all, went over, and long filaments persisted after twenty to forty days, are indicated in the fourth column. The fifth column records cultures in which the original filaments did not change in form but continued as such for twenty to forty days. The results as to the production of zoospores, whether many, few, or none, are tabulated under those respective heads. Where

zoospores were produced, but many or all of them did not germinate, the numbers are placed in the column headed *Ungerm.*

TABLE IV.

Pressure 96 $N \times 10^{-4}$ or 16.19 cm. Hg.

Solution	Cultures	Palmella		Filaments	Spores				Died
		All	Few		Many	Few	Ungerm.	None	
K	6	..	..	6	6	..	..	..	..
A	6	..	..	6	6	..	..	..	..
B	6	..	..	6	6	..	..	..	..
C	6	..	..	5	5	..	2	..	1
D	6	..	..	5	5	..	..	..	1
E	7	..	1	6	5	2	..	..	1
F	1	..	..	1	1	..	..	..	..
G	1	..	..	1	1	..	..	..	..
H	1	..	..	1	1	..	..	..	..

Pressure 193 $N \times 10^{-4}$ or 32.37 cm. Hg.

K	3	..	..	3	3	..	3	..	..
A	3	..	3	..	2	1	2	..	..
B	3	..	..	3	3	..	3	..	..
C	3	..	..	3	3	..	3	..	..
D	3	..	..	3	3	..	..	..	..
E	2	..	..	2	2	..	..	..	..

Pressure 482 $N \times 10^{-4}$ or 81.27 cm. Hg.

K	4	..	1	3	..	..	3	..	..
A	3	3	..	..	3	..	3	..	..
B	3	3	..	..	3	..	3	..	..
C	3	3	..	..	3	..	3	..	..
D	3	..	3	..	3	..	3	..	..
E	3	..	2	1	1	..	2	..	..

Pressure 964 $N \times 10^{-4}$ or 161.86 cm. Hg.

Solution	Cultures	Palmella		Filaments	Spores				Died
		All	Few		Many	Few	Ungerm.	None	
K	7	3	1	2	7	..	6	..	..
A	6	1	4	1	6	..	3	..	..
B	6	4	..	2	6	..	3	..	..
C	6	3	3	..	3	3	3	..	..
D	6	2	3	1	6	..	3	..	..
E	6	..	4	2	2	3	2	1	2
F	1	..	1	..	..	..	..	1	..
G	1	..	1	..	..	1	1	..	..
H	1	..	1	..	1	..	..	..	..

Pressure 1928 $N \times 10^{-4}$ or 323.71 cm. Hg.

K	6	3	2	1	2	4	4	..	..
A	5	3	1	1	1	2	1	2	..
B	5	5	..	..	2	..	2	3	..
C	5	5	..	..	2	3	3	..	..
D	5	3	..	..	..	3	1	..	2
E	5	..	2	..	..	..	..	2	3

Pressure 2892 $N \times 10^{-4}$ or 487.59 cm. Hg.

K	1	1	..	..	..	..	..	1	..
A	3	2	1	..	..	1	1	2	..
B	3	3	..	..	..	2	..	1	..
C	3	2	1	..	..	2	2	1	..
D	3	2	1	..	..	..	..	3	..
E	6	1	..	..	..	..	..	2	5
F	1	..	1	..	..	..	..	1	1
G	1	..	..	..	..	..	..	..	1
H	1	..	..	..	..	..	..	..	1

General Remarks on Table IV.

The only solutions in which death regularly ensued were the more concentrated ones made from single salts; *i e.*, E, F, G, H. But in almost every case where the original filaments died they evinced a great tendency to change into the palmella form

before death ensued. Often they did not die until they had actually taken the palmella form. Where a definite response was not observed before death, the cultures are recorded in the column headed *Died*. The graphic arrangement of the numbers in this table is even more striking than that in table III. The conclusions to be drawn from the above set of results will be given in the same order as were those derived from the experiments upon the palmella form.

1. *Nature of the stimulus.*—The stimulus with which we have to deal is always of an osmotic nature. Indeed, this generalization would have been expected from the nature of the stimulus affecting palmelloid cells, and from the data which we are now considering the same facts can be cited in its support.

2. *Response in vegetative growth.*—Filaments placed in the weakest solution used (pressure 96 $N \times 10^{-4}$) continued indefinitely to grow without change in form. No going over to palmella was observed until time enough had elapsed for great concentration of the solution through evaporation. The rule is, if filaments are left in a dish without renewal of fluid, they change to the other form at the end of a period of thirty to fifty days. By this time the culture is often nearly dry. Also, by addition of water from time to time filaments may be kept growing in a dish as long as one chooses. So there is little room for question as to what the nature of the stimulus producing this very tardy response really is. With higher osmotic pressures the ability of the alga to continue as filaments rapidly decreases, the first indication of such an effect being the blunting of the terminal cells. A limiting pressure for free filament growth lies apparently somewhere in the region between the pressure of 193 $N \times 10^{-4}$ and 482 $N \times 10^{-4}$. With a pressure of 964 $N \times 10^{-4}$ only eight out of forty cultures showed good growing filaments after thirty days, while many of these cultures had lost all vestige of them within that time. Not a single one of twenty-two cultures having a pressure of 2892 $N \times 10^{-4}$ showed typical filaments at the end of such a period, and there were only four which showed filaments at all. As in the other form,

an absolute limit to the production of filaments was not found. A comparison of the limit found here with that found in the case of palmella material will be made later. Filaments floating on a strong solution change to the palmella form much more slowly than those at the bottom of the dish.

The morphological details of the response just discussed are as follows. If a filament be placed in a strong solution the oldest cells are the first to be visibly affected. They continue rounding up beyond the barrel-shaped stage and become nearly or quite spherical. This process is accompanied necessarily by a splitting of the common walls from their margins inward, until, when the cells have attained the spherical form, they are practically free from one another (*figs. 4, 5*). They may not break entirely apart, however, but may remain clinging together in loose strands. The limitation upon the direction of new walls (*cf.* discussion of the responses of palmella form, *p. 300*) is now apparently removed, and the cells proceed to divide in all directions. The new cells may separate entirely (*fig. 10*), may remain loosely attached to one another (*fig. 34*), or may form an irregular parenchyma-like colony (*figs. 6, 11*). In the latter case the rounding is of course incomplete, but such cells are always nearly isodiametric. Cell division goes on much more slowly in the palmella form than in the filamentous.

3. *Response in reproduction.*—The response is the same here as in the other forms and is equally marked. The pressure limit to the production of zoospores by the filamentous form is somewhat above $964\ N \times 10^{-4}$. The limit to their germination into long filaments is below $482\ N \times 10^{-4}$. Zoospores are produced here in the way already described. The length of a filament, even in a weak solution, is limited by the fact that its oldest cells are continually becoming zoosporangia and thus losing their contents (*fig. 16*).

General considerations.

The question which this research was undertaken to answer has been answered very clearly as far as the answer goes. The

stimulus to which the alga responds by a change of form is a change in the osmotic pressure of the surrounding fluid. This must be accompanied by a corresponding change in the relation of water to the protoplasm. Whether or not extraction of water brought about by solutions of non-electrolytes or by evaporation from a moist substratum will be accompanied by the same response as that brought about by a solution of electrolytes, my experimentation has not yet gone far enough to show. It is worthy of remark, however, that when found wild this alga was in the palmella form, and was growing in air on moist bark. Loeb[8] has recently brought about artificial parthenogenesis, both in the eggs of echinoderms and annelids by placing them in a solution which would extract water from them osmotically. The result was the same whether electrolytes or non-electrolytes were used. Thus in these eggs the phenomena of segmentation and growth are profoundly influenced by osmotic pressure. Whether or not his results have any connection with those given in the present paper is an open question. The recent work upon various grains and forage plants by Buffum and Slosson[9] furnishes data which may have a somewhat closer connection with my own. Absorption by seeds, their germination, and the growth of the plant were all greatly retarded in a strong solution and accelerated in a weak one. And this was true without regard to the chemical nature of the dissolved substance; a number of electrolytes were used and also non-electrolytes. On the other hand, my experiments have not been at all in accord with those of Copeland (*loc. cit.*) when he found, with peas, maize, and

[8] Loeb, J.: Further experiments on artificial parthenogenesis and the nature of the process of fertilization. Amer. Jour. Physiol. **4**: 178. 1900.

———: Artificial parthenogenesis in annelids (Chætopterus). Science N. S. **12**: 170. 1900.

[9] (1) Slosson, E. E., and Buffum, B. C.: Alkali studies II, Bulletin 39, Wyoming Exp. Sta. 1898.

(2) Buffum, B. C.: Alkali studies III, Ninth Ann. Report, Wyoming Agric. Exp. Sta. 1899.

(3) Slosson, E. E.: Alkali studies IV, same. 1899.

(4) Buffum, B. C., and Slosson, E. E.: Alkali studies V, Tenth Ann. Report, Wyoming Agric. Exp. Sta. 1900.

buckwheat, that K-ions are osmotically more potent than any other ions in his nutrient solutions. Some erratic cultures in my series seem to support his statements, but no generalization can be made from them. Of interest, also, in this connection are the recent researches of Yasuda.[10] Working with infusoria, he finds that these organisms are able to adjust themselves to solutions of quite high concentration, and that, in general, the limit to their power of adjustment seems to be osmotically about the same, no matter what salts are used. In other words, the limit is apparently one of osmotic pressure. It is probable that many of the so-called chemical or nutritive effects of dissolved substances upon the plant organism may turn out, upon further investigation, to be wholly or in part osmotic.

In a weak solution vegetative growth is very much more rapid than in a strong one This may be due to the fact that in a strong solution the water content of the protoplasm is reduced in amount below the limit for optimum lability. When the plant grows fastest and best, it is in the filamentous form. In the weak solution, where activity seems to be at a maximum, the ions of the electrolytes, which are essential for metabolism, are not plentiful. This may suggest how the cylindrical form of cell with its increased surface[11] may be advantageous. At any rate, we may be sure that the greater surface of the cylinder puts the plant into better condition for exchange of material with its surrounding medium. On the other hand, the more concentrated solution not only withholds water from the cells, but presents a demand upon them for water. The cell meets this in part by offering as small a surface as possible to the solution. In this case, although the requisite ions may be present, and even in the right number, the scarcity of water in the

[10] YASUDA, ATSUSHI: Studien über die Anpassungsfähigkeit einiger Infusorien an concentrirte Lösungen. Jour. Coll. Sci. Imp. Univ. Tokyo **13**: 101–140. 1900.

[11] In a cylinder, the lateral surface is greater than that of a sphere of the same volume, as long as the ratio of the length to the diameter equals or exceeds 2.727. In typical filament cells of this alga the ratio of the diameters is 3, and it is often 4 and even greater. It is seldom less than 2.8. Thus it is shown that the filament cell offers more surface to the surrounding medium through its lateral walls alone, than does the palmella cell of equal volume.

protoplasm may so decrease the lability that rapid growth is impossible.

What may be the mechanics of this rounding up of cylindrical cells when placed in a concentrated solution is one of the most important problems suggested by the present research. The fact that the dead cellulose membrane is almost entirely reshaped during this process, without being dissolved, renders it probable that the change in form is directly caused by some turgor change within the cell. In a rounding cell the membrane moves and changes its form and, since it is entirely inert, the source of this motion must be either in the activity of the protoplasmic body itself, or it must be in the turgor pressure of the mass of liquid within. But since protoplasm and cellulose wall can be parted so readily during plasmolysis, the first alternative is well-nigh untenable. If the wall be forced into the spherical shape by a change in the pressure from within, this must be brought about by a change in the mass of the contained liquids. Now, this slight change in mass which might produce a change in the turgor of the cell is most probably due to an alteration in the amount of cell sap within the vacuole. When the surrounding medium suffers change in concentration, a change in the volume of the vacuole may come about through the protoplasmic sac, either secreting liquid or acting merely as a semipermeable membrane.

When filaments are placed in a concentrated solution their behavior suggests at once partial plasmolysis. Water may be extracted, the turgor pressure on the walls may be decreased, and by the forces of surface tension and cohesion the protoplasm may tend to round itself up into a sphere. If this be true, we have an explanation of the lateral bulging which accompanies the longitudinal shrinking of the cellulose envelope. If the protoplasm tended to assume a spherical form within the cylindrical wall, the pressure upon this would be decreased first at the angles. At the same time it would be relatively increased upon the lateral walls near their middle. Thus would come about a bulging of the lateral walls outward, and hence a shortening of

the cell and a drawing of the end walls towards each other. But the internal pressure is to be counted as almost nothing at the angles, while it is still considerable in the middle of each end wall. So the margins of the end walls would approach the middle of the cell more rapidly than do their central portions, and splitting of the common membrane of two adjacent cells would necessarily ensue. Several facts were observed in the cultures which seem to support some such hypothesis as the one just stated. I have placed filaments in a solution where they were completely plasmolyzed and killed without any change in form. In solutions a little less concentrated they are not plasmolyzed but round up rapidly and soon die, often in the palmella condition. With a still lower pressure the filament cells round up more slowly and live. Another fact suggesting this idea is that floating filaments can resist a stronger solution, and can resist it longer, than sunken ones. The former are to some extent in contact with the air, and thus present less surface than the latter to the liquid. Still another observation bearing upon this hypothesis of partial plasmolysis is that cylindrical cells are the only ones which are able to change their form after they have become mature. A spherical cell must remain so till it divides, even if it be in a solution of very low pressure. Only two other observations with which I am acquainted bear upon this question: Yasuda (*loc. cit.*) says infusoria in concentrated solutions tend to approach the spherical form, and Klebs (*loc. cit.*) notes that the form of *Stigeoclonium tenue* with which he was working had a tendency to produce round cells in a concentrated solution. The very marked response in the orientation of the planes in segmentation may be traceable to the change in the form of the cell, or it may not. The observed fact is that vegetative cells under low osmotic pressure divide only across their long axis (across the axis of a lateral outgrowth in the case of a branch), while under the influence of high osmotic pressures the cells divide in all directions. It is remarkable, too, that the stimulus determining the position of walls in vegetative division also brings about the extreme segmentation which occurs in the

zoosporangium. Perhaps this fact is attributable to the increased general activity in weak solutions. It has no relation to the form of the cell, since zoospores are produced from both spherical and cylindrical cells, as well as from those of intermediate shape.

My approximations to the pressure limits for the different responses are given in table V. The numbers are all coefficients of $N \times 10^{-4}$.

TABLE V.

	Maximum limit to free production of filaments	Maximum limit to production of any long filaments	Minimum limit to free production of palmella form	Minimum limit to production of any palmelloid cells	Maximum limit to free production of zoospores	Maximum limit to any production of zoospores	Maximum limit to free germination of zoospores
From palmella	1928	2892	2892	964	964	1928	964
From filaments	193	482	1928	482	1928	2892	193

From table V it will be observed that with the exception of the limits for zoospore production, all are much higher for the palmella form than for the filamentous. Perhaps the palmella cells become attuned to conditions of high pressure, so that after they have existed under these conditions for some time they are enabled to form filaments, and maintain them, at a higher pressure than was possible previously. Buffum and Slosson (*loc. cit.*, 3) state that there was a continual increase in the salt content of seeds which were imbibing water from a salt solution. Thus the difference between internal and external pressures in the case of seeds is being gradually decreased, and this means that the effect of the external pressure in retarding absorption of water is gradually diminishing also. Now if this be true in these algal cells, we may have in it an explanation of the fact that the palmella form (always growing in concentrated solutions) becomes to a greater or less extent attuned to the effects of high pressure; the ratio of internal to external pressure may be nearer unity for a palmelloid cell than for a filamentous one. That the nature of the protoplasm itself is changed by prolonged subjection to the

action of a concentrated solution is indicated by a comparison of the maximum concentrations for zoospore germination in the two forms. Zoospores from a palmelloid cell are able to produce and maintain filaments at a much higher pressure than can those produced from a filament. The two kinds of zoospores are physically alike, but are physiologically very different. It needs to be said here that in cases where the tables record ungerminated zoospores there are also many which did germinate to form filaments of several cells. In cultures so marked, however, the majority of zoospores failed to germinate in that way.

Summary.

My results are as follows:

1. The responses of *Stigeoclonium* (*tenue* ?), both in form and in reproductive activity, which accompany a change in concentration of the Knop's solution in which it is growing, are due to changes in the osmotic pressure of the medium, and are in no way functions of its chemical composition.

2. A high osmotic pressure affects the plant in four ways: (*a*) it decreases vegetative activity; (*b*) it inhibits the production of zoospores; (*c*) it causes cylindrical cells to become spherical; (*d*) it frees the alga from certain limitations as to the orientation of planes of cell division.

3. A low pressure has the following effects: (*a*) it increases vegetative activity; (*b*) it accelerates the production of zoospores; (*c*) it causes forming cells to become cylindrical; (*d*) it determines the orientation of the planes of cell division.

4. A zoospore which has come to rest responds in the same way as a palmelloid cell.

5. Cells of the palmella form become slightly attuned to the high external pressures of concentrated solutions and exhibit some responses quantitatively different from those of filaments.

In closing I wish to express my thanks to Professor F. C. Newcombe, of the University of Michigan, for much valuable suggestion and advice in the inception of the work, and to

Professor C. R. Barnes, of the University of Chicago, for aid in its completion. Also, I take occasion here to acknowledge with thanks much kind assistance regarding physical chemistry rendered me by Dr. K. E. Guthe, of the University of Michigan.

THE UNIVERSITY OF CHICAGO.

EXPLANATION OF PLATES XVII AND XVIII.

All of the figures are reproductions of photomicrographs taken with a Zeiss camera and Zeiss microscope. The first five are magnified about 450 diameters, the rest only about 140. All but *figs. 1–5* were taken as the plants lay in or upon the nutrient medium in the culture dish. The others were made from slide mounts in water.

PLATE XVII.

FIG. 1. Typical palmella form. *a*. Vegetative cell, showing clear area not covered by chloroplast. *b*. The same, but preparing to produce zoospores. *c*. Cells which have divided, but whose daughter cells are not yet separated.

FIG. 2. Typical filaments.

FIG. 3. Zoospores, immediately after they have come to rest. The clear area is the part of the periphery not bounded by the chloroplast.

FIGS. 4 and 5. Typical filaments changing to the palmella form by rounding and separation of cells.

FIG. 6. Culture no. 50. Exposure May 10. Typical palmella material. The mass at the right shows a parenchymatous colony. This was used for original material in many of the following cultures.

FIG. 7. Culture no. 144*a*. Palmella from no. 50 put into K, 96 $N \times 10^{-4}$ May 4, 1900. Exposure May 28. Original palmella masses with long filaments at periphery. Also young filaments from zoospores. The original masses are out of focus.

FIG 8. Culture no. 147*a*. Palmella from no. 50 put into C, 96 $N \times 10^{-4}$ May 7, 1900. Exposure May 28. Original masses have grown out into long filaments whose older cells have rounded. Many young filaments from zoospores.

FIG. 9. Culture no. 132*a*. Palmella from no. 50 put into K, 1928 $N \times 10^{-4}$ May 7, 1900. On May 23 many new filaments had been produced from zoospores but were rapidly breaking up. Exposure June 12. None of the original material is shown, the new filaments are almost entirely palmella. Compare this with *fig. 12*, which is from the same culture, exposure on the same day, but shows the original material. It has multiplied much, and one filament is shown reaching out from the edge of the old colony.

FIG. 10. Culture no. 141*b*. Palmella from no. 50 put into C, 964 $N \times$

10^{-4} May 7, 1900. Exposure June 12. Filaments have grown from the original palmelloid cells but these break up as soon as the cells become a few days old. Original material is seen at the upper left.

FIG. 11. Culture no. 126*a*. Palmella from no. 50 put into K, 2892 $N \times 10^{-4}$, May 7, 1900. Exposure May 28. Typical palmella form.

FIG. 12. See explanation of *fig. 9*.

FIG. 13. Culture no. 128*a*. Palmella from no. 50 put into B, 2892 $N \times 10^{-4}$ May 7, 1900. Exposure May 28. Typical palmella form. Material moved slightly during exposure, but its form is well shown.

FIGS. 14 and 15. Cultures no. 145*a* and 145*b*. Both these cultures palmella from no. 50 put into A, 96 $N \times 10^{-4}$ May 7, 1900. Exposure May 28. Filaments radiate from the original colonies and many new filaments have been formed from zoospores. In *fig. 14* the material was floating, in *fig. 15* it was resting on the bottom of the dish. The latter shows no filaments from zoospores. They usually float on the surface.

FIG. 16. Culture no. 149*b*. Palmella from no. 50 put into E, 76 $N \times 10^{-4}$ May 7, 1900. May 23 many new filaments had been formed both at edges of original masses and by zoospores. Exposure May 28. At that time the filaments from zoospores were long and their older cells were rounding up. These are shown. Zoospores and young filaments were still plentiful but did not occur in the field where the exposure was made. Many of the older cells are empty, having produced zoospores.

FIG. 17. Culture no. 139*a*. Palmella from no. 50, put into A, 964 $N \times 10^{-4}$ May 7, 1900. Exposure June 16. Zoospoores have been formed in large numbers and many have germinated, but they break apart and form palmelloid cells almost immediately. There are no filaments here more than three or four cells in length. Some resting spores which will not germinate are shown.

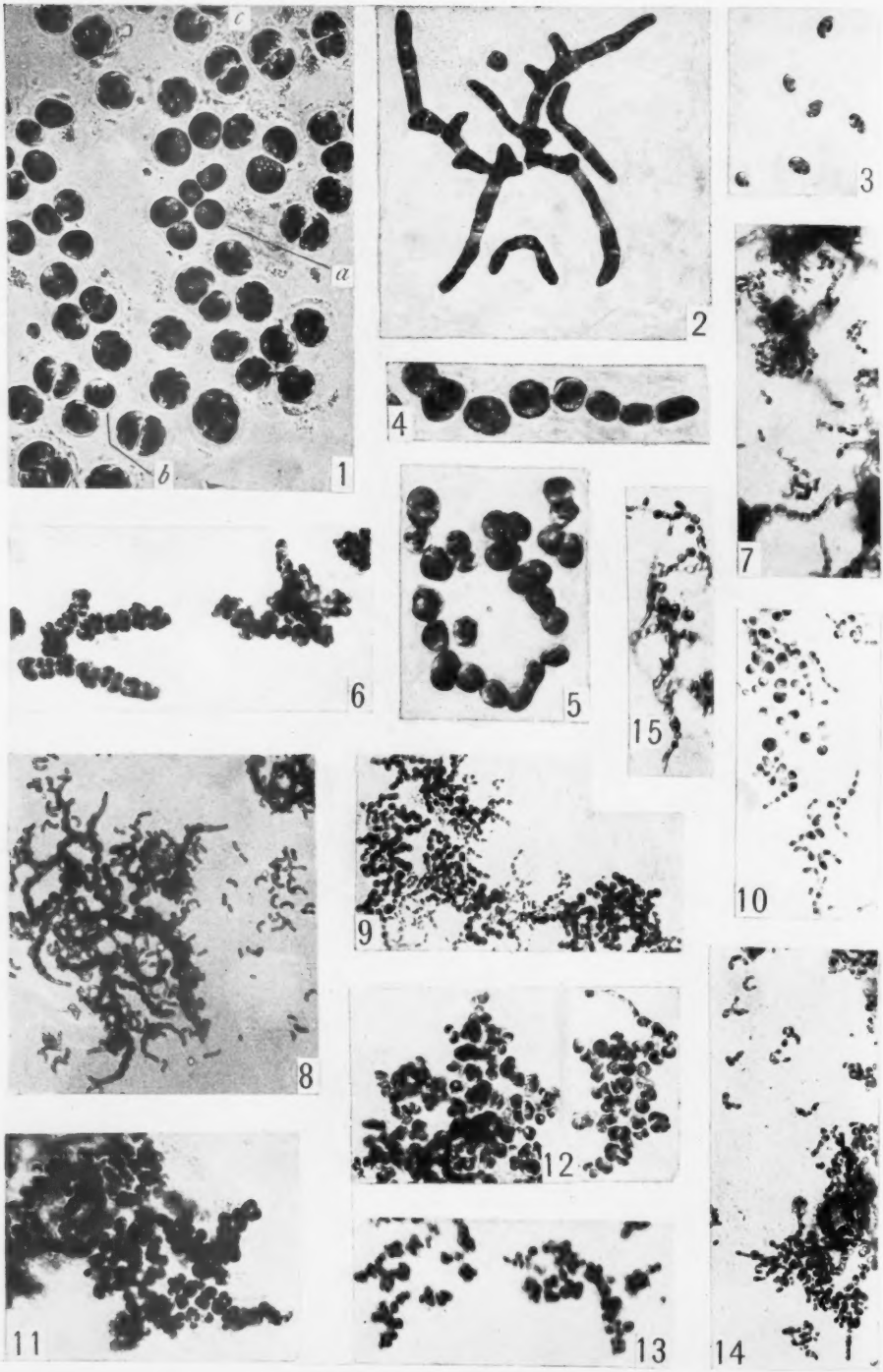
Fig. 18. Culture no. 148*a*. Palmella from no. 50, put into D, 96 $N \times 10^{-4}$ May 7, 1900. Exposure May 26. Shows typical weak solution response. Surface covered with filaments produced from zoospores.

Fig. 19. Culture no. 140*a*. Palmella from no. 50, put into B, 964 $N \times 10^{-4}$ May 7, 1900. Exposure June 15. Many zoospores were produced and germinated but went almost immediately into the palmella form. Figure shows filaments, palmella and some germinating spores.

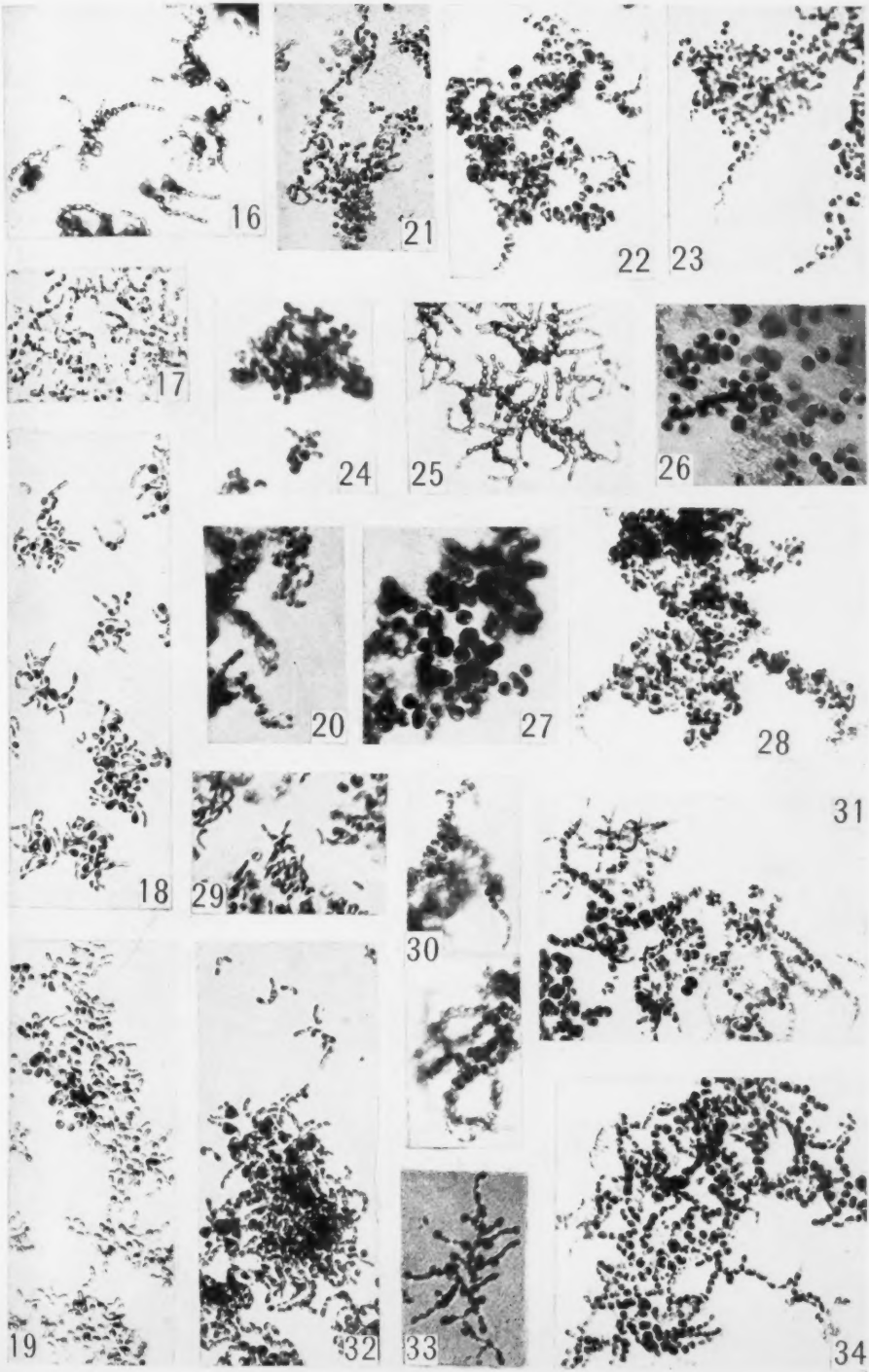
FIG. 20. Culture no. 130*a*. Palmella from no. 50, put into D, 2892 $N \times 10^{-4}$ May 7, 1900. Exposure May 28. Palmella still with scarcely any tendency to form filaments at edges.

FIG. 21. Culture no. 125*a*. Palmella from no. 50, put into E, 96 $N \times 10^{-4}$ May 8, 1900. Exposure June 15. Long filaments have been produced from zoospores. Some of their older cells are becoming rounded. Many zoospores not yet germinated are seen. Most of these germinated later.

FIG. 22. Culture no. 108*a*. Filaments from no. 83*a* (whose appearance



LIVINGSTON on STIGEOCLONIUM



LIVINGSTON on STIGEOCLONIUM

was exactly that shown in *fig. 18*), put into K, 1928 $N \times 10^{-4}$ May 8, 1900. Exposure June 15. Very few and very short filaments at the edges of large palmella masses.

FIG. 23. Culture no. 109. Filaments from no. 83*a*, put into A, 1928 $N \times 10^{-4}$ May 8, 1900. Exposure June 15. Very few filaments at the edges of large palmella colonies.

FIG. 24. Culture no. 105*a*. Filaments from no. 83*a*, put into C, 2892 $N \times 10^{-4}$ May 8, 1900. Exposure May 28. Palmella with scarcely any tendency to form filaments at edges.

FIG. 25. Culture no. 118*b*. Filaments from no. 83a, put into D, 964 $N \times 10^{-4}$ May 8, 1900. Exposure June 15, Filaments were produced from zoospores and have grown long. Their older cells have rounded and the very oldest ones are truly palmella.

FIG. 26. Culture no. 176*a*. Filaments from no. 148*a* (*fig. 18*) put into K, 2892 $N \times 10^{-4}$ May 25, 1900. Exposure June 15. Nothing but palmella.

FIG. 27. Culture no. 111*b*. Filaments from no. 83*a*, put into C, 1928 $N \times 10^{-4}$ May 8, 1900. Exposure June 15. Nothing but palmella.

FIG. 28. Culture no. 116*a*. Filaments from no. 83*a*, put into B, 964 $N \times 10^{-4}$ May 8, 1900. Exposure June 15. Very few filaments at periphery of irregular masses of palmella.

FIG. 29. Culture no. 169*a*. Filaments from No. 148*a*, put into C, 964 $N \times 10^{-4}$ May 25, 1900. Exposure June 15. A mixed culture, showing palmella, young and old filaments, the latter changing to palmella, and zoospores. The figure is poor. True palmella is shown at the upper right.

FIG. 30. Culture no. 106*a*. Filaments from no. 83*a*, put into D, 2892 $N \times 10^{-4}$ May 8, 1900. Exposure May 28. Original filaments are traced by knotted strands of palmella. At the tip of each strand are two or three filament cells.

FIG. 31. Culture no. 123*a*. Filaments from no. 83*a*, put into C, 96 $N \times 10^{-4}$ May 8, 1900. Exposure June 15. Many new filaments were produced from zoospores. The original material has, in good part, gone to palmella by increased concentration from evaporation. The younger filaments continue filaments still, but their older cells become spherical.

FIG. 32. Culture no. 120*a*. Filaments from no. 83*a*, put into K, 96 $N \times 10^{-4}$ May 8, 1900. Exposure May 28. Original material growing as filaments. No true palmella. Also many young filaments and zoospores.

FIG. 33. Culture no. 122*a*. Filaments from no. 83*a*, put into B, 96 $N \times 10^{-4}$ May 8, 1900. Exposure May 28. Original material still growing finely as filaments. Young filaments and zoospores.

FIG 34. Culture no. 158*a*. Filaments from No. 148*a*, put into H, 964 $N \times 10^{-4}$ May 25, 1900. Exposure June 15. There are scarcely any good filament cells. The palmella cells lie in loose rows, marking the direction of the original filaments.

OBSERVATIONS ON LESSONIA.

CONWAY MACMILLAN.

(WITH PLATES XIX–XXI)

THE observations recorded in this paper have been made upon a plant cast up upon the beach of Vancouver island at Baird point, on the strait of Juan de Fuca. It was collected by Miss Josephine E. Tilden, August 3, 1898, and portions of it were distributed in her *American Algæ* under the name of *Lessonia littoralis* Farlow & Setchell, this determination having been made by Professor De Alton Saunders and kindly furnished us by him. The plant when collected was apparently quite fresh, and must have been developed near the point where it was found. The day before its collection, I am informed by Miss Tilden that heavy seas had been coming in, and these no doubt dislodged the plant and carried it up upon the beach. From the shape of the holdfast it must have been growing in a cup-shaped depression of the rocks from which it had been detached without great difficulty.

The general habit and appearance of the specimen is shown in *plate XIX*, taken from a photograph made under my direction by Mr. C. J. Hibbard, of Minneapolis. The plant was removed from its tank of formalose and spread out upon a table top, which was then tilted at an angle of 50°, and the camera was lifted close to the ceiling of the room, and depressed so that the view is not appreciably foreshortened and gives a fair idea of the plant. From the holdfast to the tips of the longest laminae this specimen measured two meters in length. At the base the holdfast measures 9^{cm} in diameter. Immediately above the holdfast area the stipe is irregularly branched, developing seven principal trunks, each of which soon branches again. Owing to its probable confinement in an almost hemispherical depression, the holdfast is extremely condensed and contorted. Viewed from

below it presents in places an almost smooth fixation area, rounded off and mottled by the superposition of and compression together of the different hapteric branches. This generally bulbous base is irregular on one side, where a protruding corner of rock had entered it, and is hollow, indicating that many of the hapteric branches were turned under the base of the stem.

The main stipe can scarcely be distinguished from the holdfast by which its lower portion has been overgrown. Of the seven branches which arise the largest is 3.5^{cm} in diameter, while the smallest is 6^{mm}. All of these appear to be about the same age, and all are strongly fenestrate near the base. This, I presume, may be due to the growth of epiphytic animals and vegetation. The whole base of the plant is covered with a growth of bryozoans, together with Cladophora, Rhodymenia, and other algæ, while barnacles and sertularian hydroid colonies are growin the lacunae. It is to the growth of some of these organisms that I am inclined to attribute the lattice-like and hollow character of the stipe area near the base. Similar pathological perforations and lacunae are found on distal regions, but not so abundantly. For the most part the more distal portions of the stipe are solid, as in the tribe Lessonieæ generally. Toward the base the stipe is cylindrical, but it becomes flattened distally. Thus, 20^{cm} above the holdfast, cylindrical branches 12^{mm} in diameter are developed. Along the same branch system 10^{cm} distally, the stipe is 12^{mm} by 8^{mm} in transection. Distally 8^{cm} of this, on the same branch system, the flattening is stronger, and sections 15^{mm} by 4^{mm} are found, while the terminal portions of the stipe which give rise to the separate laminae may be but 2 or 3^{mm} in thickness and 20^{mm} in breadth. The branching throughout is dichotomous, and the paired laminae are ordinarily produced in groups of four at the tips of the flattened stipe. Each lamina has what may be called a petiolate base, and this is sometimes cylindrical in cross section, though more often flattened. The general color of the stipe and holdfast is brown, and with slight change the tint persists beyond the petioles of the laminæ. The laminæ themselves are lighter in tint, becoming quite green

in the formalose preparation, but not so different in color in the fresh material.

The laminae, of which over eight hundred are present upon the specimen under observation, vary in length from 10^{cm} on weaker lateral branches to over a meter on the stronger and central branches. They are all ribbon shaped, thin, and gradually attenuated to a point. Robust and well-developed laminae measure from 5–6^{cm} across near the base, but many of them are scarcely 1^{cm} in diameter. Some of the leaves have very well-marked midribs, while others are quite devoid of them, and it is the narrow leaves which are provided most constantly with midribs, while the broader leaves commonly do not develop them. Through the dichotomy of the plant it generally happens that two pairs of leaves are borne close together; that is the laminae appear in groups of four, of which two may be described as inner and the other two as outer. All four of the leaves may be of the slender type with midribs, or the two outer leaves may be broad and the two inner narrow. So far as this specimen shows, it is only upon the broad leaves without midribs that sori of sporangia are produced. When the midrib is present it is often very wide, reaching within 2^{mm} of the leaf-margin, but in many of the slenderer leaves the midrib is only one third the diameter of the whole lamina. There is a difference, too, between the broad and narrow leaves in their bases, the broad ones being often rounded, while the narrow ones are attenuate. Sori, when present, form patches 10^{cm} or more in length on both sides of the broad-based sporophylls. Two or three such sori are found in succession upon larger sporangium-bearing laminae, and give a somewhat blistered appearance to the leaf, owing to the characteristic loosening of the cuticle common to all Laminariaceæ.

The presence of two kinds of leaves has been already noted in other members of the genus, and the explanation given in some instances has been that the leaves are biennial. During the first year they fail to produce sporangia, but later, during the second year of their life, sporangia are produced upon them.

This is the explanation given by Areschoug[1] of the leaves of *Lessonia nigrescens* Bory. In *Lessonia fuscescens* Bory the older leaves are two-horned at the apex,this being caused by the carrying away of the upper part when decayed, as described by Hooker and Harvey.[2] In this species the sorus itself falls away from the frond and the old leaves must present a very different appearance from the younger ones. In *Lessonia littoralis* the larger leaves have lost their tips, but this does not seem to be due to a sloughing off of the sori, since the position of the latter is basal. The position of the two kinds of leaves in the species under consideration makes it somewhat difficult to believe that their difference is purely a matter of age. Unfortunately young material is not at hand, and this, as well as a large number of other interesting questions, must be held in abeyance. It is true that the sporophylls are more coriaceous than the slender sterile leaves, and as will appear in the histolological portion of this paper the general structure of the sporophyll is nearly equivalent to that of the midrib in sterile leaves. Nevertheless, from the very constant position of the leaves upon the ultimate branches of the stipe, it is difficult to assign them different ages unless some modification of the ordinary development by basal splitting has arisen. Indeed some evidence of this may be derived from the specimen under observation, in which very often but a single lamina of the narrow form appears in the notch between two of the broad laminae, and in a few instances the single central lamina is split at the base, thus giving it two petioles. It is therefore possible to conceive how by the continued growth of the plant the pair of leaves of one year may be separated by the pair of the succeeding year. This again is very much as described for *Lessonia nigrescens* by Areschoug in the work cited, and it may be said also of *Lessonia littoralis* with tolerable certainty that there is a "true defoliation and a true foliation."

If all laminae at the end of a branch could be regarded as a

[1] Areschoug: Observ. Phyc. **5**:8. 1884.

[2] Hooker and Harvey: Flora Antarctica **2**:457. 1847.

unit and taken into the mind without reference to their different ages, a comparison might be instituted with such forms as Alaria, in which the sporophylls are lateral at the base of the main frond. In Lessonia the two middle younger laminae would represent the central portion of the generalized lamina, while the outer pair of sporophylls occupying a lateral position would represent the wings. Year after year, during the life of the plant, the process of basal splitting, exfoliation of the tip, and dichotomy of the stipe continues and there are constantly present groups of laminae typically in fours, the two inner representing the midrib portion (in which the basal split actually occurs), and the two outer essentially marginal areas of the hypothetical single lamina. Without developmental stages, comprising a series of young plants for comparison, it is scarcely possible to settle the points that have been raised.

The genus Lessonia, founded by Bory,[3] has not a very large literature. The most entertaining account of the remarkable plants classed under this genus is that of Hooker and Harvey in the *Flora Antarctica* already cited. Here is pictured very vividly the habit of the antarctic forms as they appeared to the young Hooker upon his cruise as assistant-surgeon of H. M. S. *Erebus*, under command of Captain Sir James Clark Ross.

> This and the following are truly wonderful Algæ, whether seen in the water or on the beach; for they are arborescent, dichotomously branched trees, with the branches pendulous and again divided into sprays, from which hang linear leaves 1–3 feet long. The trunks usually are about 5–10 feet long, as thick as the human thigh, rather contracted at the very base, and again diminishing upwards. The individual plants are attached in groups or solitary, but gregarious, like the pine or oak, extending over a considerable surface, so as to form a miniature forest, which is entirely submerged during high-water or even half-tide, but whose topmost branches project above the surface at the ebb. To sail in a boat over these groves on a calm day affords the naturalist a delightful recreation; for he may there witness, in the antarctic regions, and below the surface of the ocean, as busy a scene as is presented by the coral reefs of the tropics.

Hooker goes on to say how the massive stems of *Lessonia fuscescens* have been mistaken by ship-masters for driftwood, and

[3] BORY: Duperry. Voy. Bot. Crypt. 1828.

how the Gauchoes use the cartilaginous stem for knife-handles; at the same time he gives, especially for *Lessonia ovata*, an extremely useful and accurate discussion of the morphology, and does not fail to point out several important histological facts upon which, in general, later accounts have been based. The most extensive anatomical study in the genus with which I am familiar is that of Grabendörfer,[4] whose results in a general way would apply to *Lessonia littoralis* as well as to the species of his investigation, *Lessonia ovata*. The figures given by him, five in number, illustrate but scantily the anatomical structure of the genus. I assume, also, that they were made from dried material, and the very different detail which I have found, and present in the accompanying plates, may be regarded as the result of studying material practically equivalent to fresh. The method of preserving large algæ in use at the University of Minnesota has not yet broken down in a single instance, although over a thousand jars of formalose material are on the shelves. Four per cent. solution of formalose is used, but after the first few months the jars are opened and fresh preservative substituted. After this it is our experience that disintegration does not occur.

Other literature which has been used in the study of this plant and has been more or less helpful is cited below.[5]

[4] GRABENDÖRFER: Beitr. zur Kenntniss der Tange. Bot. Zeit. **43**: 641. 1885.

[5] KJELLMAN: Laminariaceæ in Engler and Prantl Pflanzenfamilien I. **2**: 242. 1893.

WILLE: Ueber die Wanderung der anorganischen Nährstoffe bei den Laminariaceen. Festschrift für Schwendener. Berlin. 1899.

WILLE: Beitr. die Phys. Anat. die Laminariceæ. Christiania. 1897.

ROSENTHAL: Zur Kenntiss von Macrocystis und Thalassiophyllum. Marburg. 1890.

WILLE: Bidrag til Algernes Physiologiske Anatomie. Stockholm. 1885.

RUPRECHT: Bemerkungen über den Bau und das Wachsthum einiger grossen Algen-Stämme. St. Petersburg. 1848.

RUPRECHT: Pflanzen aus dem nördlichen Theile des stillen Oceans. St. Petersburg. 1852.

REINKE: Beiträge zur Kenntniss der Tange. Pringsh. Jahrb. **10**: 371. 1876.

OLIVER: Sieve-tubes in Laminarieæ. Ann. Bot. **1**: 95. 1887.

WILLE: Zur Anatomie von *Macrocystis luxurians*. Bot. Zeit. **42**: 801. 1884.

SETCHELL: On the classification and geographical distribution of the Laminariaceæ. Trans. Conn. Acad. **9**: 333. 1893.

MACMILLAN: Observations on Nereocystis. Bull. Torr. Bot. Club **26**: 273. 1899.

Histology.—The anatomical study of *Lessonia littoralis*, herewith presented, is based upon a series of slides made for me at my request by Mr. Harold L. Lyon, Instructor in the Botanical Department of the University of Minnesota. The material was all passed through the alcohols and embedded in paraffin in the usual way. The sections were cut upon a Minot precision microtome, and transferred gradually from clearing agents back to formalose water. Many of them were stained with aniline-water-safranin and aniline-blue, and permanent mounts in formalose water were prepared by sealing the cover slips at the edges. Mr. Lyon found that the ordinary mounting media distorted the sections, and after a few trials of other media he settled upon the formalose water as the best. I shall consider the different areas of the plant in order, beginning at the proximal regions.

The holdfast.—As has already been stated, the holdfast area of our specimen was much distorted and confused by the inextricable matting together and coalescence of originally separate branches. The primitive disk area was not definitely distinguished. Sections through the central and basal region of the holdfast showed a most confusing and irregular tissue, evidently the result of appression of hapteres to each other's surfaces. In cavities of the irregular mass of the holdfast some unattached hapteric branches were found, and these showed the ordinary dichotomous branching, cylindrial shape, and smooth green surface characteristic of the higher Laminariaceæ. They did not essentially differ in appearance from those of Nereocystis, described by me last year, nor from those of Laminaria previously described by Foslie and others. They measured less than 2^{mm} in diameter in ultimate branches, and forked repeatedly within narrow vertical limits. Cross sections showed them to be composed of a pretty homogeneous thin-walled prosenchymatous tissue in which the cells are of varying sizes, averaging from 6–30μ in diameter. Towards the surface the diameter of the cells lying in the radius of the cylinder is elongated, and there is a general superficial cambial area extending around the

holdfast and continuous over its tip immediately under the epidermis. The epidermal cells and the layer underneath are the only ones that take a protoplasmic stain with avidity, but the layers within these, to the number of five or six, contain numerous sharply staining chlorophyll bodies. It is apparent, therefore, that the growth in thickness of the holdfast is essentially superficial, and its whole tissue is produced from the cambial areas somewhat as is phelloderm from the cork cambium of higher plants. The epidermal cells proper are much the smallest of all those that make up the holdfast area, averaging from 5–10μ in height. There is no differentiated medullary area in the organ.

The longitudinal section of a haptere shows the customary structure, and serves to make clear that the growth in length takes place in the same way as does the growth in thickness. Toward the center of the section the cells are much elongated, running in some instances as high as one tenth of a millimeter in length. This length diminishes toward the tip of the organ, and directly under the tip a vertical section does not differ essentially in appearance from a transection. The dichotomous branching of the holdfast is due, as in Nereocystis and generally in Laminariaceæ, to the appearance of adjacent circular fields of cambium which undergo division more rapidly than the intervening and surrounding areas, so that the centers of these fields are protruded as the tips of the two new hapteric branches.

In older hapteres which have become matted together in the general holdfast mass, the walls are somewhat thickened in all the cells. Many of the cells are collapsed and distorted by pressure, and whole hapteric branches seem in places to be engulfed in the general tissue, reminding one of the appressions of hapteres to each other that often occur in other plants of the order. It does not seem probable that there is any rhythmical thickening of holdfasts or hapteres, such as takes place in the stipe of Lessonia, and produces the curious rings resembling those of an exogenous tree.

The stipe.—Very young stipe areas in Lessonia are much flattened, being morphologically nothing more than proximal areas of the lamina. As the plant grows, however, the region of the stipe undergoes a kind of secondary thickening, resulting in a ringed structure; and, by the greater thickness of the ring on one or both sides of the original flattened organ than over the edges, the whole stem changes from a flattened to a cylindrical body. The pith in all such cylindrical stems, even when they are very large, persists in its original thin and flattened structure, and does not appear in the form of cylindrical medulla as it does in Nereocystis. The pith is very often excentrically placed, and the number of rings of growth on one side may apparently be twice as many as on the other.

I have not found anywhere in the literature an adequate account of the anatomical basis of the phenomena which have been known and commented upon since the first discovery of Lessonieæ; and in the plates accompanying this paper an especial effort has been made to indicate the occasion for the ringed appearance so characteristic of the Lessonia stipe. It has long been suspected that the rings are in no sense annual rings, but it has been believed that they are connected with the development of the tufts of leaves in such a way that for each cycle of leaves there should be an additional ring of tissue developed in the older portions of the stipe. No doubt this view is correct, and from the exceedingly rapid growth of these gigantic algæ it is altogether reasonable to suppose that several rings might be produced in a single season.

Cross sections were made of a stipe 1^{cm} in diameter and nearly cylindrical in form. In this the pith was placed excentrically and measured 5^{mm} in length by 1^{mm} in breadth, and lay 2^{mm} from one side of the stem and 7^{mm} from the other. Five distinct rings of growth were apparent on one side of the pith, and but three upon the other. The pith itself looks almost precisely the same in vertical section as in cross section, and is made up of an anastomosing web of loosely interlaced filaments imbedded in gelatin and filled with reserve food materials. The pith does

not stop abruptly where the inner ring of cortical tissue abuts upon it, but occasional medullary filaments run out between the thicker walled and more compactly placed filaments of the cortex. Trumpet hyphæ, abundantly represented in younger pith, are not so conspicuous in material of this age. The characteristic sieve-tubes of Nereocystis and Macrocystis, as described by Parker, Wille, Oliver, and others, have not been seen in Lessonia. The tissue immediately outside of the pith has in cross-section much the look of sclerenchyma. The cells in longitudinal section are not conspicuously armed, nor, as one looks at the cross-section under the microscope, do they seem to lie in radial rows. The inner ring on both sides of the pith is principally composed of such cells as have been described. The transition to the next outer ring is more clearly marked in the gross structure than under the microscope, and at first I was much puzzled because the thin sections which showed the rings very conspicuously when held up to the light did not show them clearly when placed under an objective. The occasion for this seems to be that cells of the new growth are at first somewhat more armed, and in places stand in rows extending in a radial direction and at the same level. The walls, except over the ends of the arms, are very thick. This has been shown both in diagram and in camera-lucida sections in *figs. 8–16*. Cross sections taken through a region where the armed-cell tissue contains such radial rows at the same level will here and there cut eight or more cells in such a way that the whole row comes into view looking somewhat like a medullary ray. Since the different radial rows are not all cut through the central portions of the cells, most of the tissue will preserve its sclerenchymatous appearance and the "medullary rays," so-called (they are of course *not* pith rays), come out as streaks of lighter appearance in the cross section. As the new ring of growth grows older the cells shorten their arms and become more condensed in appearance. This shortening of the arms, together with a less parallel arrangement, makes the light streaks shorter, narrower, and finally indistinguishable from the structure around them in the

section. The difference then between the inner and outer face of a ring of growth lies in the more armed shape of the inner cells, and the less armed shape of the outer, and the optical characters of the more-armed cells in the tissue are rendered peculiar by their tendency to stand in radial rows for some distance at the same level. In general the outer rings show longer rays and a generally coarser structure than do the inner, while the innermost ring of all around the pith shows the rays but sparingly, and in cross section is almost everywhere strongly sclerenchymatous in aspect. In the outer zones I have seen as many as nineteen cells in one of the rays, showing that this number of armed cells stood at exactly the same level in a radial plane and were all cut directly through the middle when the section was taken. A comparison of the cross and long sections as presented in the plate should make this matter clear. None of the zones of growth, except the one immediately around the pith, are free over any considerable area from the rays resulting in the manner described. Lying outside of the outermost zone will be found the immediate products of the superficial cambium, not yet modified into the characteristic armed-cells, but presenting a more isodiametrical character. The actual cambial region seems to lie immediately under the epidermis. Throughout the cortical region and extending down to the region of armed sclerenchymatous cells chloroplastids are abundant, and the epidermal cells themselves, with the layers immediately beneath, take dense protoplasmic stains. There is probably division of cells going on in several of the layers under the epidermis, but it would seem to be more active close to the epidermis than in the deeper layers. Three or four layers of cells immediately under the epidermis are of the same prismatic shape as the epidermal cells proper, and almost as broad as high. Deeper cells become elongated in a direction perpendicular to the epidermis, and their walls become thinner. In vertical section they are seen to lie in definite rows. The distinction made by Grabendörfer between outer and inner cortex in *Lessonia ovata* seems to hold good also for *Lessonia littoralis*, but there is a gradual transition

from one area to the other, and the most abrupt demarcation is that between the inner cortex and the pith. Indeed cells which begin life as components of the outer cortex may later become modified into components of the inner cortex, as the stem thickens.

Some peculiarities of structure were noticed, especially globose thickenings where the arms of cells came together in the ray-like rows of inner cortex cells. These bodies of cell-wall substance in their position and form remind one quite exactly of similar structures common in Rhodophyceæ and recently figured for Gigartina by Miss Olson.[6] The "Hohlräume" of Grabendörfer I have not encountered in any of the sections under observation, but it is not improbable that they might exist in this species in older stipe areas. Granular cell contents are pretty abundant throughout the plant. The pith is particularly well supplied and the sclerenchymatous tissue of the inner cortex contains an abundance of granules.

In general it may be said of the older stipe of *Lessonia littoralis* that it consists of a strongly flattened pith surrounded by an inner cortex in which several zones of growth may be present, and an outer cortex consisting of a generally cambial group of cells arranged in from ten to twenty layers. Secondary thickening originates in the superficial cambial region, and the zonate appearance of a mature stem is due to the rhythmical production of more-armed and less-armed cells; but the difference between these is so slight that the optical distinction can scarcely be accounted for without taking into consideration also the peculiar juxtaposition of cells, especially in later zones, in radial rows at the same level.

Transition to the lamina.—The stipe becomes much flattened and the structure simplified in its distal portions. At the transition area, where the longitudinal rifts originate by which the laminae are separated from each other, the structure can be observed by sectioning the petiolate bases of laminae. These are sometimes nearly cylindrical, but generally more or less oval in cross section.

[6] Olson: Observations on Gigartina. Minn. Bot. Stud. **2**: 154. 1899.

In this region the pith is large, composed of slender interlacing hyphæ, the majority of which seem to run transversely. Mingled with the ordinary hyphæ of the pith web are numerous trumpet hyphæ with the well-known sieve-plates, where the flared-out ends of the cells come in contact with each other. Very many of the trumpet hyphæ run transversely in the pith web, and they are perhaps rather less abundant in the perimedullary portion where they take principally a longitudinal direction. The interstices between the hyphæ are filled with gelatin, and immediately outside of the general mass of interlocking and interlacing filaments is a sheath of sclerenchyma, between the longitudinally extended cells of which occasional pith hyphæ extend transversely. The pith in this region occupies about one third of the diameter of the cross section. The remaining area is composed of three well-marked layers. Immediately outside of the pith is the narrow band of sclerenchyma just described, an area not staining deeply with aniline-water-safranin. Outside of this sclerenchyma lies a band of fundamental tissue having the appearance of parenchyma in cross section. The contents of the cells are not strongly granular. Outside of the last mentioned region is chlorenchymatous tissue, in which the cells show a marked tendency to develop with their long axes perpendicular to the epidermis. Surrounding the whole is a characteristic epidermal layer of low prismatic cells. The longitudinal section through this area does not show a development of the armed cells so abundant in older stipe and characteristic of the zones of secondary thickening, but the layer directly under the chlorenchyma is composed of almost isodiametrical cells rapidly changing in form to elongated-prosenchymatous in passing from the periphery towards the pith. The cells immediately around the pith are very long, some of them measuring 1^{mm} from end to end, while the lumen as revealed in cross sections is sometimes not over 2μ in diameter. This condition reminds one of the similar shaped sieve-tubes of Nereocystis, which occur in the corresponding region of young stipe and lamina, but no end plates or callus has been detected in these cells of Lessonia, which in other

respects resemble the true sieve-tubes in form. There seems to be the same evidence of passive elongation and occasional obliteration that was noted in Nereocystis, and the same fragmentation of nuclei no doubt initiates the process of elongation. Upon the comparison of Lessonia with Nereocystis, it would seem reasonable to describe the "true sieve-tubes" of Wille and Oliver as modified sclerenchymatous elements of the perimedullary cortex.

The splitting of the lamina has not been definitely studied in this material, but so far as can be judged from the observations that have been made it takes place in the same manner as previously described for Nereocystis.

The lamina.— The essential structural basis of the lamina and the arrangement of the tissues indicate its complete morphological equivalence to the stipe. The pith is of course greatly extended into a narrow ribbon, the cells of which while retaining the web structure are not conspicuous for granular contents, indicating that the stipe serves in some sense as a reserve organ, while the leaf, essentially photosynthetic, uses its pith more particularly as strengthening tissue and a conduction path. On each side of the ribbon-shaped pith parenchymatous tissue is developed outside of a narrow intervening layer of sclerenchyma. Underneath the epidermis chlorenchyma cells extend, in from five to ten layers. The epidermal cells are not so low as those of the stipe, but generally show a long diameter perpendicular to the surface of the lamina. A well marked cuticle staining deeply is uniformly present. The edges of the lamina are occupied by cells (belonging in part to the pith area and in part to the cortex) with small diameter and thick walls, and these give strength to the margin. In young leaves it is probable that the midrib area is not immediately differentiated. The appearance of a midrib is caused simply by the greater thickness of the cortex along the central portion of the lamina and its somewhat abrupt thinning out at the sides. I was unable to distinguish in the pith tract any distinction between that portion which lay in the midrib and the portions on either side, nor do the cortical

cells differ in character in midrib and wings. The midrib may therefore be described in Lessonia as a central longitudinal hypertrophic cortex-area of the lamina.

The structure and development of the sorus.—The development of the sorus in *Lessonia littoralis* does not differ in any important respects from that described by many observers for other genera of the Laminariaceæ. The epidermal cells elongate into paraphyses, from the bases of which the sporangia arise. The sporangia themselves in some instances become almost as long as the paraphyses, reaching a length of 45μ, but this is unusual. Commonly they are from one half to two thirds as long as the slender paraphysal filaments, and of an elongated ellipsoid or club-like form. The zoospores are about 4μ in diameter, and have been observed in different stages of formation. A peculiar condition which I have not seen in other Laminariaceæ exists in the exfoliated cuticle. This during the extension of the epidermal cells into paraphyses has become greatly thickened, and may separate eventually after the manner described long ago by Thuret.[7] It does not always, however, in Lessonia separate as a continuous membrane, but is often broken up into pieces corresponding to the original epidermal cells and retaining a generally prismatic outline. Each paraphysis over a large area may carry on its end such a little cuticular cap.

The drawings of sections have been made by Miss Josephine E. Tilden, to whom I must express my thanks not only for this assistance, but for the specimen upon which my observations have been based.

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EXPLANATION OF PLATES XIX–XXI.

All sections not described as diagrammatic were drawn with a Zeiss camera lucida under a magnification of 600 diameters, and reduced one half in reproduction.

PLATE XIX.

Lessonia littoralis, from photograph.

[7] THURET: Ann. Sci. Nat. Bot. 1850.

PLATE XX.

FIG. 1. Diagram of end of branch bearing two pairs of leaves, the outer pair without midribs and bearing sori, the inner with midribs and without sori.

FIG. 2. Cross section of haptere showing epidermis, superficial cambium, and ground tissue.

FIG. 3. Longitudinal section of haptere through superficial area.

FIG. 4. Longitudinal section through central portion of haptere showing elongated parenchymatous cells.

FIG. 5. Section through older area of holdfast showing irregular and distorted structure due to appression and coalescence of original haptere branches.

FIG. 6. Diagram of cross section through stipe 12^{cm} above holdfast showing flat pith and zones of secondary thickening.

FIG. 7. Cross section through outer cortical area of stipe 1^{cm} in diameter showing epidermis, cambial tissue, chlorenchyma, and transition to sclerenchyma.

FIG. 8. Cross section through zone of secondary thickening showing portion of a "ray" caused by the section striking the middle of adjacent cells in a radial row; between two of the cells button-shaped masses of cell-wall substance have been developed.

FIG. 9. Section through same area as last showing two "rays" cut at slightly different levels so that the shapes of the component cells are different; the majority of the cells have been cut across their arms giving a sclerenchymatous appearance.

FIG. 10. Cross section through the zone of tissue nearest to the pith showing the absence of arms and consequently of "rays," and illustrating the general sclerenchymatous appearance of this region.

FIG. 11. Cross section through the pith of same stipe showing the anastomosing web of hyphæ with cells packed with reserve materials.

FIG. 12. Longitudinal section through outer cortex and epidermis; transition from armed to outer cells.

PLATE XXI.

FIG. 13. Longitudinal section through secondary growth zone of stipe illustrating the armed character of the cells and their arrangement side by side at the same level.

FIG. 14. Diagrammatic representation of the position maintained by the armed cells; cross sections at point *a* would show the ordinary sclerenchymatous structure, while those made at point *b* would show the "rays" as in *fig. 9*.

FIG. 15. Longitudinal section of stipe near the pith showing on the left hyphæ of the pith web, and on the right the sclerenchymatous cells of the inner growth zone.

FIG. 16. Diagram of cross and longitudinal sections through the petiolate base of the lamina; *a*, outer cortex and chlorenchyma; *b*, parenchymatous tissue; *c*, sclerenchymatous layer around the pith; *d*, pith.

FIG. 17. Detail of cross section through same area as last, showing epidermal, chlorenchymatous, and parenchymatous tissue.

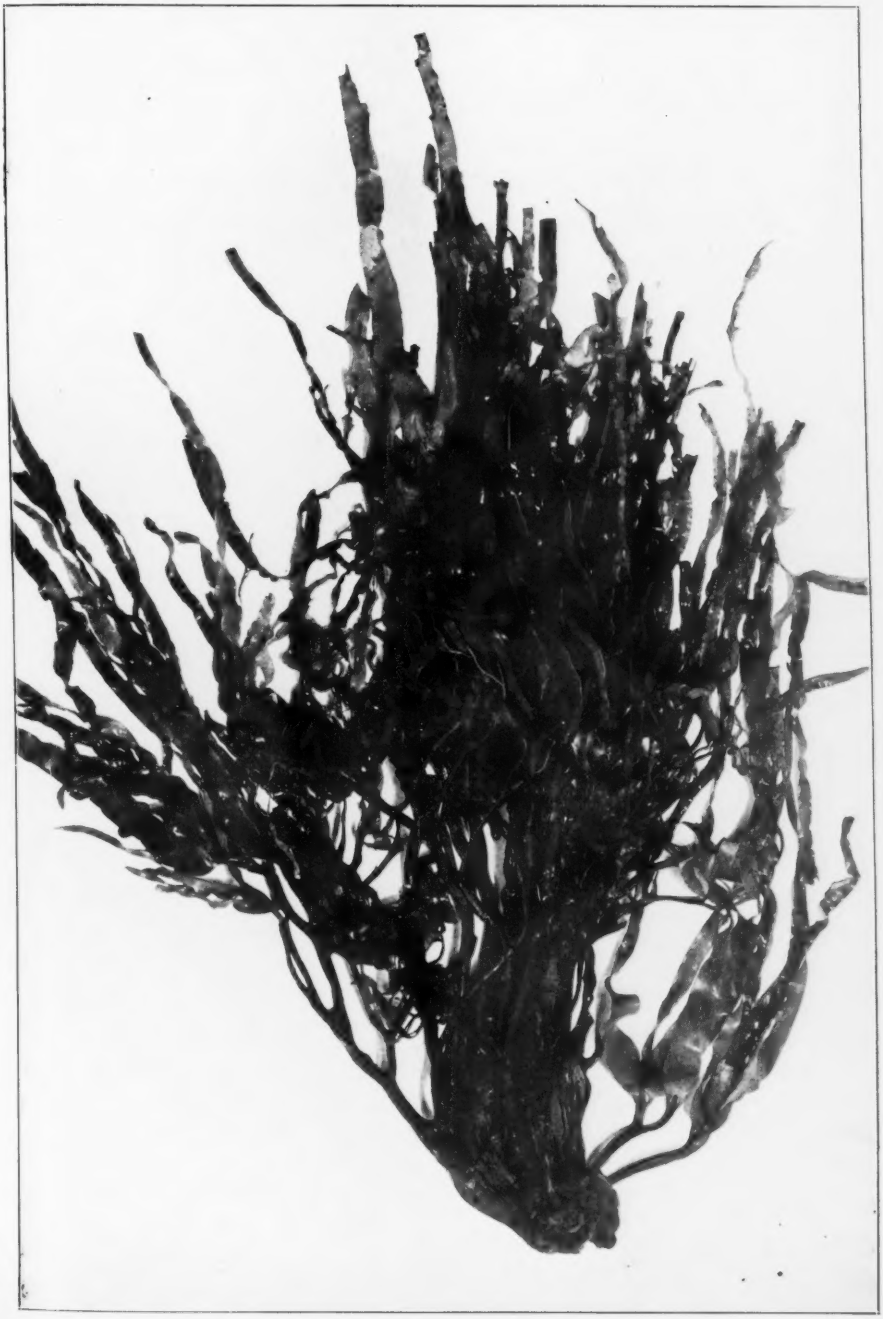
FIG. 18. Cross section same area as last and continuous with it, showing transition to perimedullary sclerenchyma with cells of the pith web running out from the central pith.

FIG. 19. Longitudinal section through the region of *fig. 17*.

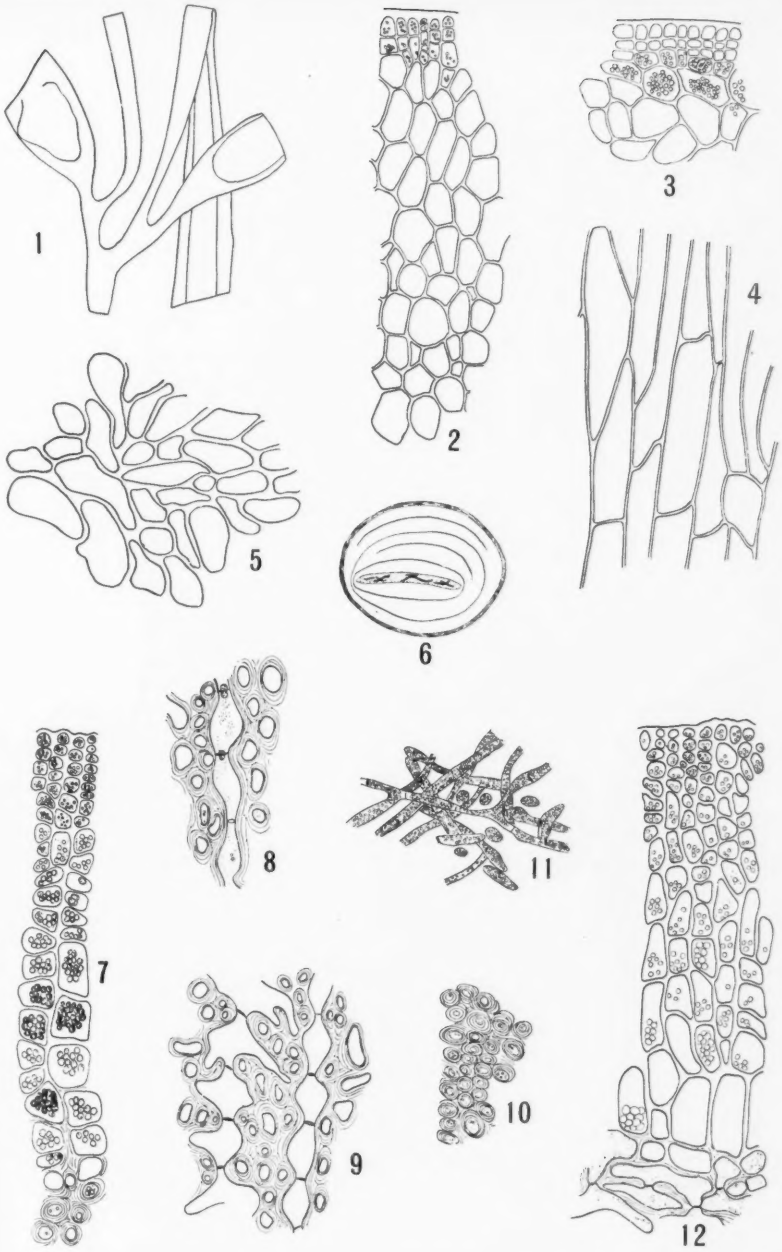
FIG. 20. Longitudinal section through the region of *fig. 18*.

FIG. 21. Cross section of lamina through the wing.

FIG. 22. Section through a sorus showing sporangia with paraphyses, the latter capped by cuticular fragments corresponding to separate cells of the epidermis.



MacMILLAN on LESSONIA



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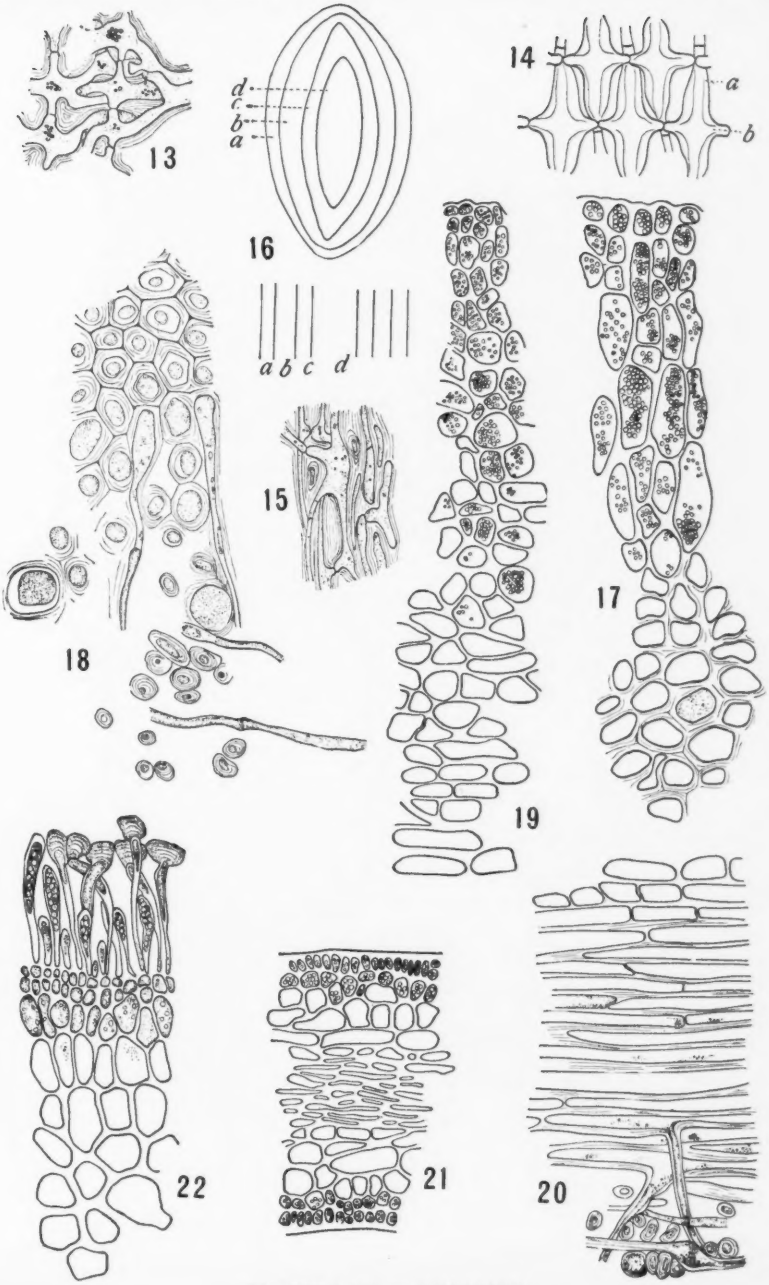

MacMILLAN on LESSONIA

STUDIES IN CRATÆGUS. II.[1]

C. D. Beadle.

Cratægus aprica, n. sp.—A large branching shrub, with one or several stems, 3–5^{m} tall, or occasionally arborescent and attaining a height of 6–7^{m} under favorable conditions: bark of the trunk and larger stems dark gray or nearly black, often conspicuously furrowed, the surface being broken into small, irregular, persistent, plate-like scales: branches ascending, armed with stout, either straight or slightly curved spines 2–6^{cm} long, which are frequently branched and of greater size on the trunk and larger branches; branchlets at first villose-pubescent, but ultimately glabrous, marked by numerous small, pale lenticels, the bark reddish-brown, after the first winter changing to gray, with tinges of red or brown, the whole forming a compact, oval, or round head: winter buds globose, bright reddish-brown, the outer scales of the terminal ones thick and pointed: leaves thin to subcoriaceous in texture, obovate, rhombic-ovate, or orbicular in outline, 1.5–7^{cm} long including the petiole, 1–5^{cm} wide, the borders dentate or crenate-dentate and conspicuously glandular, more or less lobed near the acute apex, or on vigorous shoots more deeply lobed, especially below the middle of the blade, usually narrowed but sometimes rounded at the base and prolonged into a margined petiole 7^{mm}–2^{cm} long, which, like the base of the leaf, bears numerous black colored glands; stipules linear, linear-lanceolate, or on strong shoots foliaceous and lunate, pectinately-glandular or glandular-serrate, caducous: flowers, which appear in the vicinity of Biltmore, North Carolina (type locality), when the leaves are nearly grown, borne in 3–6-flowered, pubescent or pilose-pubescent, bracteate corymbs; pedicels 1–2^{cm} long, pilose-pubescent, bearing one or two small pectinately-glandular, deciduous bractlets: calyx obconic, pubescent, at least near the

[1] Continued from Bot. Gaz. **28**: 417. 1899.

base, the divisions 3–5^{mm} long, glandular-serrate, or pectinately-glandular: petals rather broader than long, 9–13^{mm} by 8–12^{mm}, with a short broad claw at the base: stamens 10, 5–8^{mm} long, the anthers light yellow: styles 3–5, surrounded at the base with pale hairs: fruit globose, 9–14^{mm} in diameter, red or orange-red, ripening and falling after the middle of September, the flesh thick, yellowish, pleasant to the taste: nutlets 3–5, hard and bony, 6–8^{mm} long, 3–4^{mm} measured dorso-ventrally, the back ridged and grooved and the lateral faces nearly plane, a volume of 125^{cc} containing about 1598 clean and dry seeds.

Crataegus aprica has been confounded with *C. flava* Ait.,[2] from which it differs in the shape and color of the fruit. The new species is abundantly represented in the mountainous region of North Carolina, and has been found in similar situations in Tennessee, Alabama, and Georgia, inhabiting sunny exposures in dry, rocky, or clayey soils.

The type material is preserved in the Biltmore herbarium.

Cratægus sororia, n. sp.—A tree 5–7^{m} tall, with a trunk 1–1.5^{dm} in diameter, dividing two or three meters above ground into several stout, ascending or spreading branches, which form an oval or round head; or usually smaller, 3–4^{m} in height, forming a large shrub with one or more stems: bark gray, tinged with brown or nearly black, furrowed and broken on the surface into small, persistent scales: branchlets armed with gray or chestnut-brown spines 1.5–3.5^{cm} long: buds globose, bright reddish-brown: leaves 2–6^{cm} long, including the petiole, 1–3^{cm} broad, or on vigorous shoots sometimes 6^{cm} broad, obovate, round-ovate, or nearly orbicular in outline, or on the shoots even broader than long, with a truncate or subcordate base, acute or rounded at the apex, either gradually narrowed or abruptly contracted at the base and prolonged into a margined, glandular petiole 5^{mm}–1.5^{cm} long, the borders sharply and irregularly serrate and incisely lobed, especially above the middle, the serratures glandular-apiculate; sparingly pubescent when young (at least along the petiole, midrib, and principal veins), becoming glabrous, or with a few hairs in the axils of the prominent veins and bordering the

[2] Hort. Kew **2**: 169. 1789.

petiole, bright green on the upper surface, paler below, fading in the autumn to tones of yellow and brown, or with occasional dashes of red: flowers, which appear in the vicinity of Rome, Georgia (type locality), during the last of April or first of May, and when the leaves are nearly grown, borne in pubescent, glandular-bracteate 3–6-flowered corymbs; pedicels 5–15^{mm} long, sparsely pubescent, bearing one or more pectinately-glandular, caducous bractlets: calyx obconic, usually with a few soft hairs, the divisions 6–8^{mm} long, glandular-serrate: stamens normally 20: styles 2–5, commonly 3, surrounded at the base with pale hairs: fruit large, globose, 12–18^{mm} in diameter, red, red and yellow, or yellowish-red, ripening and falling after the middle of September, the flesh thick, soft, and pleasant to the taste: nutlets usually 3, hard and bony, 7–9^{mm} long, 4–5^{mm} thick, measured from the back to the inner angle, the lateral faces nearly plane and the back ridged and grooved.

Cratægus sororia is related to *C. aprica* above proposed and to *C. flava* Aiton, *l. c.* From the former it may be separated by the more numerous stamens, larger fruit and calyx segments, and coarser seeds; while from the last named species it differs from the accepted figures and descriptions which have been drawn from specimens in cultivation in Europe, in the shape of the fruit and the pubescent corymbs and petioles. The proposed species is abundantly represented on wooded hills, slopes, and rocky exposures, and in old fields from northwestern Georgia and adjacent Alabama southward to Florida.

The type material is preserved in the Biltmore Herbarium.

Cratægus Alleghaniensis, n. sp.—A large shrub 2–4^{m} tall, or infrequently a small tree 5^{m} in height: bark gray, sometimes tinged with brown or much blackened: branches ascending, armed with slender, gray or reddish-brown spines 1.5–4^{cm} long, the whole forming an oval or round head; the growth of the season clothed with reddish-brown bark and marked by small, pale lenticels: leaves ovate, oval, or nearly orbicular in outline, 2–8^{cm} long, including the petiole, 1.5–6^{cm} wide, very sharply and irregularly serrate and incisely lobed, acute at the apex, either abruptly narrowed or rounded at the base, or on vigorous shoots subcordate and prolonged into a margined, glandular petiole

5mm–2cm long, bright green on the upper surface, slightly paler below and with 3–4 prominent pairs of veins, sparsely pubescent when young, especially on the upper surface, soon becoming glabrous: flowers, which open in the vicinity of Valley Head, Alabama (type locality), the first of May, disposed in simple, 3–6-flowered corymbs; pedicels 1–2cm long, bearing one or more small, linear, or lanceolate, pectinately-glandular caducous bractlets: calyx obconic, glabrous, the divisions 4–6mm long, glandular-serrate: petals 7–9mm broad, 9–12mm long, the claw at the base narrow: stamens normally 10, 4–6mm long, the anthers purple: styles 2–5, mostly 3–4, surrounded at the base with pale hairs: fruit, which ripens after the middle of September, globular-pyriform, red, 9–14mm long, 8–12mm broad: nutlets 2–5, usually 3–4, hard and bony, 5–7mm long, about 3mm thick measured from the back to inner angle, the lateral faces nearly plane and the back grooved and ridged.

Cratægus Alleghaniensis is abundant on Lookout mountain above Valley Head, Alabama, growing on rocky exposures or in the shade of oaks and pines. It is related to *C. aprica* above proposed, from which it may be distinguished by the less glandular foliage and inflorescence, the form and darker color of the fruit, purple anthers, and the sharply serrate borders of the leaf-blades.

The type material is preserved in the Biltmore Herbarium.

Cratægus venusta n. sp.—A tree seldom more than 8m tall, or frequently a large branching shrub growing on rocky slopes or occasionally on the banks of small streams: flowers, which open about April 20, in the vicinity of Birmingham, Alabama (type locality), and when the leaves are half grown, 2–2.5cm or occasionally more in diameter, disposed in 3–6-flowered corymbs; pedicels 1.5–2cm long, glabrous, bearing two or three pectinately-glandular, deciduous bractlets which vary from 5mm to 1.5cm in length and from 2–4mm in width: calyx obconic, smooth, the segments acute, 4–6mm long, 1.5–3mm wide, glandular-serrate or often pectinately-glandular below the middle: petals nearly orbicular, rather broader than long, 9–12mm wide, 8–10mm long, with a short and broad claw at the base: stamens normally 20, 4–8mm long, the anthers yellow: pistils 3–5, surrounded at the

base with pale hairs: fruit which ripens and falls after the first of October, globose or slightly oval, 9–13^{mm} wide, 9–15^{mm} long, dull red to greenish-red when fully ripe, sometimes, when more exposed, brighter, and frequently presenting surfaces of russet-red; the cavity 3–5^{mm} broad and nearly as deep, surrounded by the remnants of the stamens: nutlets 3–5, hard and bony, 6–9^{mm} long, 3.5–5^{mm} measured dorso-ventrally with the lateral faces nearly plane and the back grooved and ridged: leaves thin to subcoriaceous, sparsely pubescent when young, soon smooth, bright green on the upper surface, paler below, showing 4–7 pairs of prominent veins, from obovate to ovate in outline, occasionally on strong shoots round-ovate, 2.5–12^{cm} long, including the petiole, 1–6^{cm} wide, acute at the apex, rounded or narrowed at the base into a narrowly winged and remotely glandular petiole 7^{mm}–4^{cm} long; the borders irregularly or doubly serrate and incisely lobed, with minutely glandular-tipped serratures: stipules linear or linear-lanceolate, pectinately-glandular, caducous: bark of the trunk varying from ashy-gray to light-brown, slightly fissured: branches spreading or ascending, bearing numerous stout, dark chestnut-brown, or gray spines 3–7^{cm} long, or the older branches and frequently the trunk armed with strong much branched spines of greater size; the bark reddish-brown, marked by small, pale lenticels: buds globular, bright reddish-brown.

Cratægus venusta is abundantly represented in the Red Mountain region of Alabama, where it was apparently first discovered by Mr. C. L. Boynton of the Biltmore Herbarium, and later by Professor C. S. Sargent of the Arnold Arboretum. The new species is closely related to *C. Sargenti* Beadle,[3] differing mainly in the more numerous-flowered corymbs, shorter and stouter pedicels, yellow anthers, narrower and less persistent calyx lobes, and the strikingly obovate and elongated outline of the larger leaves.

The type material is preserved in the Biltmore Herbarium.

Cratægus Ashei, n. sp.—A tree seldom attaining a height of more than 6^{m} or commonly a large branching shrub with one or more stems: bark of the trunk and older branches light gray or reddish-brown, smooth on the smaller plants, fissured and

[3] Bot. Gaz. **28**: 407. 1899.

slightly scaly on the trunk of larger individuals: branches ascending, armed with stout, simple or branched, gray or chestnut-brown spines 2–5^{cm} long, forming a pyramidal or oval head; branchlets at first pubescent, becoming smooth, the bark reddish-brown or gray, sprinkled with small, pale lenticels: buds globular, bright reddish-brown, the terminal on strong shoots with thick, acute, slightly spreading scales: leaves, which are about half grown at flowering time, ovate, round-ovate, or occasionally obovate, 3–9^{cm} long including the petiole, 2–6^{cm} wide, or occasionally larger on vigorous shoots, rounded or acute at the apex, abruptly contracted or wedge-shaped at the base and prolonged into a margined, pubescent petiole 5^{mm}–2^{cm} long, which, as well as the base of the blade, bears several sessile or stalked dark colored glands, the borders sharply and often doubly serrate, the serratures tipped with minute black glands, the upper surface pubescent, becoming nearly smooth with age, bright green and lustrous, pale green on the lower surface, more densely and permanently pubescent, especially along the midrib and principal veins, which are displayed in 5–7 pairs, texture firm to nearly coriaceous; stipules narrowly lanceolate, straight or falcate, frequently foliaceous and lunate on vigorous shoots, pectinately-glandular or glandular-serrate: flowers, which expand in the vicinity of Montgomery, Alabama (type locality), early in May, produced in simple or branched 3–10-flowered, glandular-bracteate, pubescent corymbs, 1.5–2.5^{cm} in diameter: calyx obconic, pilose or pubescent, the divisions lanceolate, 7–10^{mm} long, 3–5^{mm} wide, smooth or nearly so on the outer surface, pubescent on the inner, pectinately-glandular or incisely glandular-serrate, reflexed after anthesis: petals slightly broader than long, 10–14^{mm} by 9–12^{mm}: stamens normally 20, 6–9^{mm} long, the anthers yellow: styles 3–5, surrounded at the base with pale hairs: pedicels 1.5–3^{cm} long, pubescent or pilose, bearing a linear or lanceolate, pectinately-glandular bractlet: fruit, which ripens and falls the last of September and early in October, red, more or less pubescent, globose, 10–14^{mm} in diameter or occasionally slightly oval; cavity 4–6^{mm} wide, surrounded

by the persistent calyx lobes and remnants of the stamens: nutlets 3–5, hard and bony, displaying a prominent ridge on the back, or conspicuously grooved and ridged, 6–9^{mm} long, 4–6^{mm} measured from the back to inner angle, the lateral faces nearly plane.

Cratægus Ashei has been found in the abandoned fields and woodlands, generally in clayey soil, of Montgomery county, Alabama. The species is related to *C. Harbisoni* Beadle,[4] from which it may be distinguished by the comparatively simple and less floriferous corymbs, more lucid and less pubescent foliage, and by the attenuated calyx lobes. I take pleasure in associating with this species the name of Mr. William Willard Ashe, forester of the geological survey of North Carolina.

The type material is preserved in the Biltmore Herbarium.

Cratægus senta, n. sp.—A small tree 5–6^{m} high, or more frequently a large shrub with one or more stems, bark of the trunk rough, dark gray, usually much blackened near the base: branches spreading, slightly pendulous or recurved, zig-zag, clothed with smooth, dark or brownish-gray bark and armed with stout, gray or chestnut-brown spines 1.5–6^{cm} long: leaves obovate, obovate-cuneiform, or on vigorous shoots round-ovate to nearly orbicular, 2–7^{cm} long including the petiole, 7^{mm}–5^{cm} wide, prolonged into a margined, glandular petiole 5^{mm}–2^{cm} long, the borders deeply and irregularly serrate and incisely lobed, especially above the middle of the blade, the serratures glandular-tipped, bright green and shining on the upper surface, pale below and displaying several pairs of conspicuous ascending veins, pubescent at the time of unfolding, soon becoming nearly glabrous, except on the petioles and in the axils of the prominent veins, and fading to tones of yellow, red and brown: flowers, which appear early in May in the vicinity of Biltmore, North Carolina (type locality), and when the leaves are nearly grown, borne in simple, pubescent 3–6-flowered corymbs; pedicels 1–2.5^{cm} long, densely pubescent when young, bearing one or two linear, caducous bractlets: calyx obconic, pubescent, the divisions 4–6^{mm} long, glandular-serrate: petals 8–12^{mm} in diameter, rather longer than broad, the claw at the base short and

[4] Bot. Gaz. **28**: 413. 1899.

broad: stamens normally 20, 5–7^{mm} long: styles 3–5, surrounded at the base with pale hairs: fruit globose, 10–14^{mm} in diameter, red, ripening and falling the last of September and beginning of October: nutlets 3–5, hard and bony, 7–9^{mm} long, 4–5^{mm} measured from back to inner angle, the back shallowly grooved and the lateral faces nearly plane.

Cratægus senta is abundantly represented in abandoned fields and in open woods near Biltmore, North Carolina, and was referred to by me in an article published in the BOTANICAL GAZETTE[5] under the name *C. elliptica*. The new species is related to *C. Michauxi* Pers.[6] (*C. glandulosa* Michx.,[7] not Aiton or Wildenow), from which it may be recognized by the longer petioles and pedicels, the sharply cut and nearly smooth leaves and less glandular characters of foliage and inflorescence.

The type material is preserved in the Biltmore Herbarium.

Cratægus Alabamensis, n. sp.—A tree 4–6^{m} tall, or more commonly a large branching shrub with one or more stems, and spreading, often pendulous branches: bark rough, gray tinged with brown, or much blackened near the base: branchlets at first villose-pubescent, often puberulous in their first winter, but ultimately glabrous, gray tinged with reddish-brown, or even brighter on the younger wood, slender, zig-zag, armed with dark gray or chestnut-brown spines 1.5–4^{cm} long, or sometimes longer and branched on the older branches and trunk: winter buds globose, bright reddish-brown: leaves obovate or obovate-cuneiform, rounded at the apex and often with a short point at the end of the midrib or occasionally very abruptly contracted into an acute tip, gradually narrowed or cuneiform at the base and prolonged into a margined, pubescent, glandular petiole 7^{mm}–2.5^{cm} long, 2–7^{cm} long including the petiole, 1–3.5^{cm} wide, or even larger on the shoots, pubescent at the time of unfolding, especially along the principal veins, and at maturity subcoriaceous or thinner, bright green and lustrous above and pale on the lower surface, the borders crenate-dentate or serrate, especially above the middle, glandular-serrate or entire near the base; stipules linear or linear-oblong, on the strong shoots

[5] BOT. GAZ. **25**: 447. 1898.

[6] Syn. Plant. **2**: 38. 1807.

[7] Flora Bor.-Am. **1**: 288. 1803.

lunate or variously lobed, pectinately-glandular or glandular-serrate, caducous: flowers, which appear when the leaves are almost fully grown, borne in simple or branched, 3–9-flowered, densely-pubescent corymbs, and open in the vicinity of Montgomery, Alabama, (type locality), early in April; pedicels 1–2.5^{cm} long, densely pubescent, bearing one or more small, glandular, caducous bractlets: calyx obconic, pubescent, the divisions 6–8^{mm} long, glandular-serrate, reflexed after anthesis: petals orbicular or longer than broad, about 1^{cm} in diameter, with a short and broad claw at the base: stamens normally 20, 5–7^{mm} long, the anthers yellow: styles 2–5, usually 3, surrounded at the base with pale hairs: fruit large, elongated, 1.5–2^{cm} long, 1–1.5^{cm} wide, red, ripening early in August: nutlets usually 2–3 hard and bony, 8–10^{mm} long, 3–4^{mm} measured from the back to the inner angle, the lateral faces nearly plane and the back grooved and ridged.

Cratægus Alabamensis is abundant in dry, clayey soil near Montgomery, Alabama, growing in open woods or in cleared grounds. It is evidently related to *C. Michauxi* Pers. *l. c.*, from which it differs in form and size of the fruit, less glandular foliage, and attenuated calyx segments.

The type material is preserved in the Biltmore Herbarium.

Cratægus pinetorum, n. sp.—A shrub 1–5^{m} tall growing in dry or rocky woods where the prevailing forest growth consists of pines, oaks, and hickories: stems one or more, clothed with smooth or roughened, dark gray bark, which is frequently blackened near the base: branches slender, armed with slender, straight or curved, dark gray or chestnut-brown spines 1–5^{cm} long, the growth of the season covered with smooth, reddish-brown bark which is marked by small pale lenticels, becoming in the second year dark gray tinged with brown: leaves ovate, oval or obovate, 2.5–9^{cm} long including the petiole, 1.5–5^{cm} wide, sparingly pubescent on the midrib and veins on the upper surface when young, soon glabrous, acute at the apex, sharply and irregularly serrate and incisely lobed, the serratures minutely glandular-apiculate, narrowed or rounded at the base and prolonged into a margined, sparsely-glandular petiole 1–2.5^{cm} long,

thin in texture, bright green on the upper surface, below paler and displaying 3–5 pairs of ascending, prominent veins; stipules linear or linear lanceolate, glandular, caducous: flowers, which open in the vicinity of Albertville, Alabama (type locality), about the first of May, and when the leaves are nearly grown; produced in simple, glandular-bracteate 3–6-flowered corymbs; pedicels 1–2^{cm} long, bearing one or more narrow, pectinately-glandular, caducous bractlets; calyx obconic glabrous, the divisions 3–5^{mm} long, glandular-serrate: petals orbicular, or a little broader than long, about 8–10^{mm} in diameter: stamens normally 20, 4–6^{mm} long: styles 3–5, surrounded at the base with pale hairs: fruit, which ripens in September, subglobose, 7–10^{mm} in diameter, changing from tones of green and yellow to light red when fully ripe, the flesh thin: nutlets 3–5, hard and bony, 5–7^{mm} long, 3–4^{mm} measured from the back to the inner angle, the lateral faces nearly plane and the back ridged and grooved.

Cratægus pinetorum is probably related to and easily contrasted with *C. Boyntoni* Beadle[8], from which it may distinguished by the smaller fruit and more numerous stamens.

The type material is preserved in the Biltmore Herbarium.

Cratægus rubella, n. sp.—A shrub 1–4^{m} tall, growing in upland woods: stems one or several, much branched, clothed with gray or reddish-brown bark, either smooth or slighly fissured and scaly: branchlets numerous, armed with slender, straight or slightly curved gray or chestnut-brown spines 1.5–4^{cm} long, or on the older plants nearly destitute of spines back to the larger branches: leaves oval, ovate or obovate, 3–9^{cm} long including the petiole, 1.5–4.5^{cm} broad, thin at first, becoming firm in texture, sparingly pubescent when young especially on the upper surface, soon glabrous, sharply and doubly serrate to near the base, and incisely lobed above the middle of the blade, acute at the apex, narrowed at the base and prolonged into a margined, sparsely-glandular petiole 1–2.5^{cm} long, reddish-green or purplish at the time of unfolding, becoming bright green above, paler below and fading with decided tones of yellow; stipules oblong

[8] Bot. Gaz. **28**: 409. 1899.

or linear-lanceolate, pectinately-glandular, early deciduous: flowers, which appear when the leaves are nearly grown, borne in simple, 3–6-flowered glandular-bracteate corymbs, and opening in the vicinity of Valley Head, Alabama (type locality), about the first of May; pedicels 1–2 cm long, bearing one to three pectinately-glandular, deciduous bractlets: calyx obconic, the segments 4–6 mm long, glandular-serrate: petals rather broader than long, 8–12 mm wide, 7–10 mm long, with a short, broad claw at the base: stamens normally 10, sometimes united in pairs and appearing to be fewer, 5–7 mm long, the anthers light purple: styles 2–4, rarely 5, surrounded at the base with pale hairs: fruit red, pyriform or oval, 12–15 mm long, 10–12 mm wide, ripening after the middle of September: nutlets 2–3, rarely 4–5, hard and bony, 6–7 mm long, 3–4 mm measured dorso-ventrally, the lateral faces nearly plane and the back ridged and grooved.

Crataegus rubella is abundant on Lookout mountain above Valley Head, Alabama, growing in the shade of oaks and pines, and has been collected in similar situations in eastern Tennessee and western North Carolina. It has been customary to refer this species to *C. flava*, *C. rotundifolia*, and *C. coccinea*, but I am inclined to place it near and compare it with *C. Boyntoni* Beadle, *l. c.*, from which it differs conspicuously in the outline of the leaves, shape and color of the fruit, and the purple color of the anthers.

The type material is preserved in the Biltmore Herbarium.

Cratægus straminea, n. sp.—A low shrub, about 1 m in height, frequently growing in large patches in upland woods, or occasionally attaining larger proportions, 2–3 m tall, and developing from one or more stems a coarse shrub with loose or straggling outline: branches gray, tinged with brown or reddish-brown, armed with slender, curved or straight spines 1.5–6 cm long which vary from gray to chestnut-brown in color: leaves oval, ovate or round-ovate in outline, acute at the apex, abruptly contracted or rounded, or on vigorous shoots truncate or subcordate at the base, acutely incised or slightly 5–9 lobed, and sharply and irregularly serrate except at the extreme base of the blade, the serratures glandular-apiculate, thin to subcoriaceous in texture, 2.5–10 cm long including the petiole, 1.5–6 cm broad, sparingly

pubescent when young, becoming glabrous with age, or with a few hairs along the midrib and principal veins which are disposed in 3–5 pairs; petioles winged, 7 mm–3.5 cm long, bearing several or many stalked glands; stipules linear or linear-oblong, pectinately-glandular, caducous: flowers, which appear in the vicinity of Valley Head, Alabama (type locality), and when the leaves are nearly grown, disposed in glandular-bracteate, 3–6-flowered corymbs; pedicels 7 mm–2.5 cm long, bearing one or two, pectinately-glandular, caducous bractlets: calyx obconic, the divisions 4–6 mm long, glandular-serrate and with a few stalked glands below the middle: petals nearly orbicular, 6–10 mm in diameter, with a short, broad claw at the base: stamens normally 10, 5–7 mm long, the anthers purplish: styles 3–5, surrounded at the base with pale hairs: fruit subglobose or pyriform, 10–13 mm high, 9–11 mm wide, yellow or greenish-yellow, ripening after the middle of September: nutlets 3–5, hard and bony, 7–8 mm long, 3–4 mm measured from the back to the inner angle, the lateral faces nearly plane and the back grooved and ridged.

Crataegus straminea frequently covers large areas on the top of Lookout mountain above Valley Head, Alabama, growing in the shade of oak, pine, and hickory trees, and will probably be found to extend into the adjacent regions of Tennessee and Georgia. It is related to *C. Boyntoni* Beadle, *l. c.*, from which it differs in habit of growth, form and color of fruit, color of the anthers, slender spines, and leaves with more sharply cut borders.

The type material is preserved in the Biltmore Herbarium.

Biltmore Herbarium,
Biltmore, N. C.

BRIEFER ARTICLES.

DAVID FISHER DAY

(WITH PORTRAIT)

JUDGE DAVID F. DAY, who died on August 21, 1900, was born in Buffalo, N. Y., in 1829, and his whole life was spent in that city. For more than fifty years he was engaged in the practice of the law, in which profession he held high rank.

His love of nature, which was that of an enthusiast, early led him to the study of the natural sciences, in which he became most proficient. As a field botanist he was excelled by few. Gifted with a remarkable memory and a particularly clear conception of the relationships of families and genera, he was able to place a new plant with a facility that I have seldom seen equaled. His methods of reasoning upon botanical problems were not always the methods of the schools, and his way of approaching a question from an unusual standpoint was refreshing and often the means of solving difficulties of long standing. The fact that he was not a professional botanist seems to have deterred him from publishing many of his observations and deductions, which were of great interest and value.

In connection with Judge Clinton he made a thorough study of the local flora, and the result appeared in "A catalogue of the plants of Buffalo and vicinity," published in 1883. Later he prepared a list of plants growing on the reservation at Niagara Falls, which was published by the state. He was one of the founders of the Buffalo Society

of Natural Sciences, and a life-long member of it. To him also is due the credit of establishing the Buffalo Botanic Garden, in which he was particularly interested.

His library was a notable one, as he was a collector of rare discrimination, and the works on botany were many and valuable. In addition to the more pretentious volumes, a large collection of pamphlets was accumulated, among which appear a very large number of local catalogues. These books of botanical interest, as well as his collections of living plants and herbarium specimens, he was preparing to transfer to the Botanic Garden when he was stricken down.

Mr. Day had for years been a member of the Park Commission of his city, and drew the act which created the Park department. In this act, drawn thirty years ago, he made provision for both botanical and zoological collections, both of which, after years of waiting, he saw established.

His loss will be mourned by the many botanists of his acquaintance, as well as by his fellow-citizens, by whom he was held in high esteem. —JOHN F. COWELL, *Buffalo Botanic Garden.*

OBSERVATIONS ON THE ROOT SYSTEM OF CERTAIN CACTACEÆ.

THOSE who make botanical trips into arid regions do so generally with the one idea of collecting material to be worked up at leisure in laboratories or herbaria, or to be deposited in botanic gardens. Their stay, as a rule, is closely limited, and the necessity of covering a great amount of ground brings with it a tendency to pass over those details which take considerable time. The root system of desert plants, both as regards structure and distribution of roots, is one of those questions which has perforce been to a great extent neglected, our knowledge, generally speaking, being confined to the examination of the amount of underground growth collected with herbarium specimens. Therefore it seemed to me worth while during my stay in Tucson, Arizona, in the midst of the great cactus plains, to make a rather careful study of the roots of certain large forms which could scarcely be preserved *in toto*.

The root systems of Cactaceæ, in general, are somewhat smaller than would be expected. The distribution, however, is such as in a way to make good the deficiency in size and length. The specific

examples here cited may be fairly taken, I think, as types, as without exception they agree in general characters.

Echinocactus Wislizeni Engelm.— Plants about 7.5^{dm} high and 3.5 to 4^{dm} in diameter gave the following results. Three or four main roots, 10 to 12^{mm} thick, branch out horizontally from beneath the plant, taper but slightly, are sinuous and much branched at the tips, in such a manner as pretty thoroughly to cover the ground about the plant within a radius of 2.4^{m}. The fine rootlets are very numerous, generally turning upward. In no place does this set of roots run much more than 10^{cm} below the surface. Just beneath the plant are a few small roots passing almost directly downward, tapering very rapidly, and with numerous branchings penetrating to the depth of scarcely 30^{cm}.

Opuntia fulgida Engelm.— An arborescent form. A specimen about 15^{dm} high, considerably branched, showed, as in the above case, several long slender roots with fine branches, running horizontally 5 to 10^{cm} below the surface, and covering an area with a radius of 30^{dm} about the plant. In a plant of *O. fulgida mamillata* (Schott) Coulter, which was washed by a small torrent, these roots appeared above ground in many places. In both of these specimens a few quickly tapering roots were demonstrated at the base of the plant, passing directly downward to the depth of about a foot.

Opuntia Whipplei Engelm. showed a similar state of affairs.

A Platopuntia (*O. angustata* Engelm.?) possessed much the same characters. The prostrate younger joints here send out roots and reproduce by innovation,[1] but the chief roots are to be found attached to the oldest living joint. At this point a double system can be seen, consisting of a couple of large roots, horizontal and but slightly below the surface, and one or two much smaller roots passing downward with rapid branching.

Cereus giganteus Engelm.—This plant thrives on rocky hillsides, and its root system is modified somewhat by conditions of soil and slope. In the specimen examined the roots which passed directly downward came very quickly in contact with a flaky bedrock, into the crevices of which they sent their branches, sometimes causing a splitting off of fragments. Although these roots seemed to pass scarcely three feet downward, their hold was exceedingly firm. The horizontal roots were directed almost entirely up the slope, sometimes appearing on the surface, but often descending to some little depth to avoid large

[1] TOUMEY, J. W.: Vegetal dissemination in Opuntia. BOT. GAZ. **20**: 356. 1895.

bowlders. The area which they covered extended about 45^{dm} away from the plant, which was between 12 and 15^{m} high.

Cereus enneacanthus Engelm.—This rather ascending, cespitose form showed, as in the other cases, the two sets of roots; horizontal, long and sinuous; and vertical, abruptly tapering and much-branched. Several specimens were examined.

Conclusions.—In the majority of the larger Cactaceæ there are two distinct root systems—one horizontal, for absorptive purposes; the other passing downward, for anchorage. The depth of the horizontal system varies with the degree of penetration of surface water, which, in turn, is to some extent dependent on the character of the soil. One of the specimens of Echinocactus was examined the day following a gentle rain which had continued intermittently for two days, thus giving the water time to soak in as it fell. The soil was dampened to a distance of about four inches below the surface, just the depth of the absorptive root system.

Observations upon young plants of *Opuntia fulgida* give the following as the sequence of root formation. The first to be developed by joint or seedling are the vertical roots, which for a time act both for absorption and anchorage. As the plant increases in size the ground directly beneath it is shielded from moisture by its body, and in order to get the necessary food material the horizontal system is developed secondarily, starting, as a rule, directly from the stem, but occasionally appearing in part as horizontal branches of vertical roots. This horizontal system covers an area far greater than that sheltered by the parts above ground. As the soil is generally firm, and the horizontal roots give some support, there is little need for any roots to descend to a great depth. The small amount of surface exposed to winds may be considered another reason for this.

Correlated with the difference in distribution of the two systems is a difference in structure, as may be proved by a most superficial examination. The horizontal roots are in all cases extremely brittle, the vertical much more elastic and capable of withstanding far greater tension. The woody cylinder in large absorptive roots is far smaller relatively than that of the anchoring roots. Microscopically this difference may be most easily seen in the secondary xylem. For this examination sections of roots of *Opuntia fulgida* and *Echinocactus Wislizeni* were used. The xylem of the absorptive root is composed mainly of ducts, that of the anchoring roots, which, after the appearance of the

horizontal system, seem to have developed for this purpose entirely, consists almost wholly of wood cells. Owing probably to the general evenness of climate the annual rings are not easily demonstrated.—CARLETON E. PRESTON, *Harvard University*.

NON-SEXUAL PROPAGATION OF OPUNTIA.

PROFESSOR TOUMEY, in an article in the BOTANICAL GAZETTE (**20**: 356. 1895), speaks in general terms of the use of spines as aids in dissemination of opuntias which are dispersed by the breaking off of the separate joints. A short note may be added as to the function of these spines, especially in such long-spined species as *O. fulgida* Engelm. A joint falling upon the sand very often rebounds from the elasticity of the spines, and by this impetus is carried some distance from the parent plant. The greatest aid, however, is in the placing of the joint. Joints destined for such dissemination are as a rule obovate, the best developed areolae with the longest spines being situated on the distal end, those of the proximal end being scarcely at all armed. The result of this is that the joint upon falling almost invariably lights with its base downward, in the best possible position for striking root. The distal parts are kept off the ground in all cases by the long spines.—CARLETON E. PRESTON, *Harvard University*.

GAURELLA = GAUROPSIS.

I HAVE to propose the restoration of the name of *Gauropsis* Torrey & Fremont (Rep. 315. 1845), to take the place of *Gaurella* Small (Bull. Torr. Bot. Club **23**: 183. 1896). Gauropsis was clearly defined by its authors, though not treated as a genus, and the type and only species was the *Œnothera canescens* Torrey & Fremont, described at the place cited. The *Index Kewensis* gives *Gauropsis* Presl, 1849; I have not seen Presl's work, but in any event it is later than that of Torrey and Fremont. The type species of Gauropsis, *Gaurella guttulata* (Geyer) Small will become *Gauropsis guttulata*, or, I think, much better *Gauropsis canescens*, since the name *canescens* is only preoccupied by a slight variety of *Œnothera biennis*.—T. D. A. COCKERELL, *East Las Vegas, N. M.*

CURRENT LITERATURE.

BOOK REVIEWS.

Fossil plants.

MORPHOLOGISTS have made but little use of the work of paleobotanists, both on account of the nature of the material and because paleobotanists too often have not been trained morphologists. The time for this feeling, however, has passed, and some of the most striking extensions of our morphological horizon have come from the work of paleobotanists. What was needed more than any thing else was the critical sifting of the vast accumulation of paleobotanical data from the standpoint of modern botany. In 1891, Count Solms-Laubach published his admirable *Fossil Botany*, which has ever since remained a standard work for botanists, although more destructive of previous claims than constructive. Very recently, however, Mr. A. C. Seward has begun his great work on *Fossil Plants*, but it has not yet included the vascular plants; Professor R. Potonié has published his *Lehrbuch der Pflanzenpaleontologie*, a very compact presentation of the subject; and M. R. Zeiller's *Éléments de Paléobotanique* has just appeared. All of these books stand for the newer paleobotany, which is to reject uncertain evidence and rest upon a foundation of morphology.

What the morphologist wishes, however, is the omission of details which are not pertinent to him, and the compact presentation of what paleobotany has definitely contributed to morphology. This has been done, and apparently well done, by Professor D. H. Scott, in a book which has just appeared.[1] His purpose has been "to present to the botanical reader those results of paleontological inquiry which appear to be of fundamental importance from the botanist's point of view." Since the important results have related almost entirely to pteridophytes and gymnosperms, the *Studies* are restricted to them. It is certainly true that Professor Scott has presented in a remarkably clear way just what botanists wish to know, but his data must be judged by paleobotanists. The book must be read for details, but some of the most striking suggestions for the consideration of morphologists are as follows.

The remarkable elaboration of Equisetales and Lycopodiales in the Paleozoic is fully set forth, and should form a part of every morphological presentation of these groups, the living representatives being totally inadequate for such a purpose. The most suggestive conclusion in this connection, however, is that these two groups, which seem to be so far apart now,

[1] SCOTT, DUNKINFIELD HENRY: Studies in fossil botany. 8vo. pp. xiii + 533, with 151 illustrations. London: Adam and Charles Black. 1900. 7*s.* 6*d.*

are but divergent lines from an ancient stock represented by the Sphenophyllales. Professor Scott regards the Sphenophyllales as worthy to stand as a gymnosperm group of primary rank. He would include in it not only Sphenophyllum and its acknowledged associates, but Cheirostrobus as well, a genus which strikingly combines the characters of Equisetales and Lycopodiales.

Of course the Filicales are fully considered, a group of enormous antiquity, having held its own since the Silurian, and whose habit was so predominant during the Paleozoic that many plants have been included with them whose real affinities are elsewhere. In general, Professor Bower's grouping of Filicales into the Simplices, Gradatae, and Mixtae is shown to have an historical basis.

One of the most interesting sections of the book is that devoted to a consideration of the Cycadofilices, a provisional Paleozoic group made to contain forms which combine the characters of Filicales and Cycadales, and most of them first described as ferns. The representative genera are Lyginodendron, Heterangium, and Medullosa, whose habits and anatomical features are strikingly intermediate, but whose spore-bearing members are unfortunately unknown. It is evident, however, that in them we have forms which strongly confirm the conclusion that cycads have been derived from ferns.

As was to be expected, the dominant gymnosperm group of the Paleozoic, Cordaitales, is set apart as of primary rank, and, associated with the Cycadofilices, seems to furnish the background for later gymnosperm development.

The author regards the Bennettiteæ as but a very distinct phylum of the Cycadales, but to the reviewer it would appear that they are worthy of primary rank and the name Bennettitales. Their habit and anatomical structure seem to be almost identical with those of Cycadales, but the lateral sporangium-bearing shoots, the fern-like "ramenta," and more than all the remarkably modified and complex ovulate strobili and peculiar embryo, justify the claim for independence. This is further justified by the steadiness maintained by the peculiar structures throughout the numerous European forms, and in the still more extensive display of the group in the rich Mesozoic flora of the United States, from which Professor Ward has described numerous species under the generic name Cycadoidea. In this connection it is interesting to note the recent description by Dr. Wieland of the staminate strobili of *Cycadoidea ingens* Ward. The numerous sporophylls are borne upon a central axis, instead of upon a hemispherical receptacle as in the ovulate strobili, and each sporophyll bears a considerable number of linear sori, each sorus composed of twenty to forty clavate sporangia. It seems that the Mesozoic has obtained the name of the "age of cycads" from the display of Bennettitales, and that while doubtless true cyads existed, and among them the genus Cycas, they are somewhat indefinite and uncertain.

In discussing the general problem of the phylogeny of gymnosperms, the author fairly states the contending claims for its polyphyletic and monophyletic origin, but plainly inclines to the latter position. He sees no reason for imagining any connection whatsoever with the Lycopodiales, and still less with the Equisetales. The connection of Cycadales and Bennettitales with Filicales being considered as established, both through morphology and the paleobotanical evidence of such a group as Cycadofilices, "the derivation of the other gymnosperms centers about the extinct group Cordaitales," whose affinities with the Cycadales are clear.—J. M. C.

Tropical Nature.

COSTANTIN, the well-known French botanical philosopher, has issued a second volume in the series known as Bibliothèque Scientifique Internationale. His studies in various lines of botanical research, and especially his classic ecological papers on aquatic plants, have well fitted Costantin, both for his work on Adaptation-Evolution[2] and for the work which is the subject of this review.[3] In the introductory chapters the author gives a realistic picture of the virgin forest of the tropics, and vividly recounts the first sensations that one has in these new scenes. After a few remarks on tropical climates, Costantin plunges at once into the very deepest ecological problems of the tropics. He first discusses the origin of forests, and takes up some of the types of trees that are peculiar to tropical forests. An interesting chapter on leaves follows, and some of the most recent studies, as those on hydathodes, are introduced. After a few pages on flowers and fruits, the author gives a brief survey of the geological history of forests, holding to the older view that the present tropical forests are fragmentary, but yet lineal descendants of those which have passed away. The lianas come in for an excellent treatment, four chapters being devoted to a discussion of the various classes and their origin. Chapters follow on epiphytes, especially those found among the tree tops; parasites of various classes; symbiosis, one chapter dealing with saprophytes, the other with the rôle of ants and other animals in influencing plant life. Saprophytism at one time would not have been given as the type of symbiosis, but recent studies on mycorrhiza makes such a classification necessary. The strictly botanical part of the volume closes with a chapter on mangroves and one on island floras, the latter from the geographic standpoint.

Though the volume is entitled *Tropical Nature*, it is confined practically to the plant world of the tropics. The last chapter is a curious exception and

[2] Les végétaux et les milieux cosmiques (Adaptation-Evolution). 292 pp., with *171 figures* in the text. Paris. 1898.

[3] COSTANTIN, J.: La nature tropicale. 8vo. pp. 315. *figs. 166.* Paris: Félix Alcan. 1899. 6 fr.

deals with religious legends and traditions of the human race. This seems out of keeping with the rest of the work, which, though planned for a semi-popular audience, contains much matter of equal value to ecologists with the works of Haberlandt, Schimper, and Warming. The figures are crude and unsatisfactory in the extreme, when compared with Schimper. Though little that is new is to be found in Costantin's new volume, one finds there one of the best summaries we have of many topics, such as lianas and parasites. In the author's philosophy, also, is a great deal of valuable suggestion to all who are interested in ecology.—HENRY C. COWLES.

Organography.

TO THE admirably selected series of German botanical works translated into English for the Clarendon Press, the directors have now added Goebel's *Organography of Plants*.[4] This book is the only recent one dealing with morphology in its modern revival under the influence of experimental physiology. We have already written at length of the first part of this work upon its appearance,[5] and nothing need be added now.

The translation is by Professor Isaac Bayley Balfour of the University of Edinburgh, and in the main is very satisfactory. Intensification or weakening of the author's meaning occurs here and there; an occasional archaism, like "the seldom occurrence," p. 63, has crept in; now and then one finds a badly constructed sentence, as "one would naturally expect that a lateral shoot removed from the shoot system and planted vertically and which rooted would behave similarly," p. 51; and we much regret that the incorrect form "Spermaphyta" should be given further currency by the translator. But these defects are such as may be charitably overlooked in view of the great advantage of having this classic in English dress. We trust that the publication of the second part (with its promised index) will be made possible at an early day by the appearance of the remainder of the second part from the author's hand. The imprint of the Clarendon Press is guarantee that the manufacture of the book is all that can be desired.—C. R. B.

NOTES FOR STUDENTS.

M. H. DEVAUX has recently made an extensive study of lenticels, especially as concerns the physiological conditions of the growth and differentiation of their tissues, the results of which occupy two thirds of a volume of the *Annales des Sciences Naturelles*.[6]

[4] GOEBEL, K.: Organography of plants, especially of the Archegoniatæ and Spermaphyta. Authorized English edition by ISAAC BAYLEY BALFOUR. Part I: General Organography. Roy. 8vo. pp. xvi + 270. *figs.* 130. Oxford: The Clarendon Press. 1900.

[5] BOT. GAZ. **25**: 290. 1898.

[6] DEVAUX, H.: Recherches sur les lenticelles; étude sur les conditions physiologiques de l'accroissement et de la différenciation de la cellule et des tissus. Ann. d. Sci. Nat. Bot. VIII. **12**: 1–240. *pl.* 6. 1900.

The memoir is too voluminous to permit an adequate summary in the space at command, and the original should be available in every laboratory where research is prosecuted. Devaux gives a résumé of his work in the final chapter, from which some extracts are here made.

Lenticels are found in all the great groups of vascular plants and on all their organs which have secondary growth. The primary number on the stem is in ratio with the vigor of growth (indicated by the length of shoots or internodes), with the total number of internodes, and with the numerical rank of each internode. The curve of their production agrees closely with the curve of elongation of the internode, though the maxima do not exactly coincide. In each internode the lenticels are almost always more numerous on the distal moiety. The dimensions attained by lenticels depends directly on their number per unit of surface.

Two types are distinguished: (1) the closing layers are few in number, consisting of cells intimately united, with no (or small) intercellular spaces, being oftentimes comparable to true cork; (2) the closing layers are numerous, composed of rounded cells with many large intercellular spaces, and are like the packing cells (*Füllzellen; cellules comblantes*), but suberized. The packing cells are alike in both.

As to origin, lenticels are primary or secondary. Primary lenticels are formed early and at points determined by an organ (stoma, rootlet, less often a bud). Secondary lenticels are formed later and at points not determined by an organ. Whenever stomata are present there is a tendency to produce lenticels below them, usually in the cortex, sometimes in the pericycle. If stomata are very numerous, partial or complete abortion of some lenticels may occur. Some stems, wanting stomata, produce lenticels late, in the neighborhood of a bud after the fall of the leaf. Lenticels are likewise generally produced at the base of young rootlets, though equally subject to abortion. Lenticels are continually growing and continually being destroyed. The growth is due to continuous proliferation of the cells, the destruction to death or suberization of the cells. For the most part, proliferation produces complete rupture of the closing layers, especially in the spring, followed by hypertrophy, death, or suberization (accompanied or not by sclerosis), and by centripetal displacement of the cambium or its transformation into permanent tissue, to be regenerated later at a deeper level.

The lenticels are usually porose, but sometimes a complete closure occurs, not in winter only but throughout the year. Thanks to this porosity they certainly serve in large measure in the general gaseous exchanges of the organs. But it would be false to say that the lenticels exist for these exchanges. For (1) they are often absent or insufficient; (2) often the plant has porose regions different from lenticels; (3) opening and closing of the lenticels is not due to the needs of aeration. Rather they are organs of transpiration and automatic regulators of the internal moisture, which the

plant uses efficiently for the proper gaseous exchanges also. (M. Devaux promises a further memoir on the general aeration of the plant by lenticels.)

Finally, lenticels are defined as small limited regions of the superficial parenchyma in continual proliferation and continual development, capable of hypertrophy or of cicatrization, according to the conditions of external or internal humidity.—C. R. B.

A RECENT PAPER[7] on the embryology of *Taxus baccata* fills in some of of the gaps in previous accounts. The writer secured an abundance of wild material, but employed rather primitive methods in making his preparations, fixing in absolute alcohol, imbedding in celloidin, and staining in haematoxylin. The following is a brief résumé of his work.

The origin of the aril shows it to be a second integument. In tracing the development of the embryo sac the author was not able to get the earliest stages. The two, four, and eight-celled stages of the embryo sac were not observed, but many sacs were observed in later stages. Free nuclear division continues until there are about 256 free nuclei in the sac (the eighth division), when cell walls begin to appear. These cells rarely contain more than one nucleus, and have a regular six-sided appearance in optical section. In the later stages of endosperm formation the cells are often multinucleate. The formation of archegonia begins at the end of May or the first of June, but archegonia in very different stages of development are soon found in the same prothallium, even embryos and young archegonia often appearing together. The usual number of archegonia is from five to eight, but nine, ten, and even eleven were observed. Pollination occurs from the beginning to the middle of March, and there is no so-called pollen chamber. By the end of May three nuclei can be seen in the pollen tube, the tube nucleus, and the nuclei of the stalk cell and of the generative cell. Shortly before fertilization occurs the generative cell divides into two very unequal cells. Fertilization takes place about the first of June. There may be several pollen tubes, and several "archegonia" may be fertilized. The sex nuclei, which are of about the same size, come into contact and then sink to the bottom of the archegonium, where fusion takes place. Nuclear division then proceeds until there are from ten to sixteen free nuclei at the base of the archegonium, after which the free cells become arranged into tiers, the upper tier ("rosette"), the middle tier, consisting of suspensor cells usually six in number but sometimes more, and the lower tier, which is the embryo proper. In *Taxus baccata* all the suspensors of one archegonium belong to a single embryo. There are normally two cotyledons, but in one case three were observed.—CHARLES J. CHAMBERLAIN.

[7] JÄGER, L.: Beiträge zur Kenntniss der Endospermbildung und zur Embryologie von *Taxus baccata* L. Flora **86**: 241–288. *pls. 15–19.* 1899.

KAHLENBERG AND AUSTIN have been continuing the earlier researches on the toxic action of various substances on seedlings. They conclude[8] that the toxicity of acid sodium salts is greater than it ought to be if it were due solely to H ions and that the theory of electrolytic dissociation is unsatisfactory in explaining the poisonous action of these acid salts and of acids as well. The true explanation, they suggest, is very likely to be found in the ability which the substances all have in common, to neutralize basic substances. This explanation is independent of the theory of electrolytic dissociation. Kahlenberg also found himself unable to explain the sour taste of acids on the basis of the H ions[9] and holds the physiological effect to be due to their chemical activity in virtue of the fact that the H is replaceable by a metal of a basic radical. The more readily the H is replaced, the more reactive the acids are and the more intense is their taste.—C. R. B.

DR. GINO POLLACCI published a year ago the results of some of his researches on photosynthesis[10] which have not been adequately noticed in this journal. His most important results are as follows:

Green organs of plants which grow in sunlight give the aldehyde reaction with Schiff's reagent. Under the same conditions fungi do not so react; nor do leaves, kept for some hours in darkness or in an atmosphere free of CO_2. Formic aldehyde reactions are also obtained from expressed sap by proper treatment. He holds, therefore, that formic aldehyde is produced by green organs under the normal conditions of photosynthesis, and promises to give the results of his researches on the process of its formation in a second memoir—C. R. B.

THE CORRECTION of a large number of typographical and other errors, both of omission and commission, in Engler and Prantl's *Pflanzenfamilien*, especially in the general index, will be found in *Allgemeine Bot. Zeitschrift* 1900: 110 *et seq.* Otto Kuntze and Tom von Post are the ferrets. Though inclined to magnify and multiply the errors, which they figure at 9315 (!), they have done a service for bibliographic work which will doubtless save users of the *Pflanzenfamilien* some hours and much bad temper.—C. R. B.

[8] Jour. Phys. Chem. 4: 553–569. 1900. [9] Jour. Phys. Chem. 4: 533–537. 1900.

[10] Atti Instituto Botanico de Pavia N. S. 7:(1–21). 1899.

NEWS.

MR. CYRUS A. KING, formerly of Summerville, Mass., has been appointed instructor in botany in Indiana University.

R. WILSON SMITH, Ph.D. (University of Chicago), instructor in McMaster University, Toronto, during the past year, has just been promoted to the full professorship of botany in that institution.

DR. OSCAR LOEW, late of the Department of Agriculture at Washington, has received and accepted a call to become again the professor of agricultural chemistry in the University of Tōkyō. He sailed October 8.

DR. B. M. DUGGAR, assistant cryptogamic botanist of the Agricultural Experiment Station and instructor in botany in Cornell University, has returned from a year's study in Germany and has been promoted to an assistant professorship.

PROFESSOR DR. A. B. FRANK, director of the biological section of the Imperial Sanitary Bureau, formerly director of the institute for plant physiology in the Royal Agricultural School at Berlin, and author of a well-known text-book of botany and many physiological papers, died on September 27, at the age of 62.

ABBÉ A. B. LANGLOIS died at St. Martinville, La., on August 1. His long and indefatigable study of the flora of Louisiana was prosecuted in such leisure as could be obtained in the course of his parish duties. He has supplied material most liberally for the study of specialists in all groups, and his name has been used for many new species which he discovered. His cryptogamic collections were probably left to the Catholic University at Washington, to which several years ago he gave his phanerogamic plants.

THE UNDERSIGNED requests all foreign botanical writers to send to him a copy of each of their publications, as far as possible, and especially reprints of botanical articles published in proceedings, transactions, and other journals of learned societies. This request is made in order that foreign botanical literature may be reviewed promptly for Just's *Botanischer Jahresbericht*, thus bringing the same to the early notice and general use of all botanists.—PROFESSOR DR. K. SCHUMANN, *Botanischer Museum, Berlin, W.*

THE FOLLOWING report of the sixth annual meeting of the Botanical Society of America, which was held in New York City, June 26 to 28, 1900,

has just been received from the secretary. For the reading of papers the society met in joint session with Section G of the American Association for the Advancement of Science, June 28, in room 502, Schermerhorn Hall, Columbia University. The meeting of the sections was called to order by the vice president, William Trelease, who announced the arrangements for the joint session, and called B. L. Robinson, president of the society, to the chair. The retiring president, L. M. Underwood, then read his address, "The Last Quarter: A Reminiscence, and an Outlook." The full text of the address has been printed in *Science*.

Following is the program of papers presented:

The significance of transpiration, *C. R. Barnes;*

Relationship and variability of the Adirondack spruce, *Charles Peck;*

Nuclear studies on Pellia, *B. M. Davis;*

On the structure of the stem of *Polytrichadelphus dendroides*, *Mrs. E. C. Britton;*

Observations on the group Yucceæ, *William Trelease;*

Spermatogenesis in the gymnosperms, *J. M. Coulter;*

The pollen tube, and division of the generative cell in pines (by invitation of the council), *Miss M. C. Ferguson;*

On the homologies and probable origin of the embryo-sac, *George F. Atkinson;*

Observations on Lessonia, *Conway MacMillan;*

Thigmotropism of roots, *F. C. Newcombe;*

Starch in guard cells, *B. D. Halsted;*

Coenogametes, *B. M. Davis;*

The development of the archegonium, and fertilization in the hemlock spruce (by invitation of the council), *W. A. Murrill;*

The causes operative in the formation of silage, *H. L. Russell* and *S. M. Babcock;*

A closed circuit respiration apparatus, *H. L. Russell* and *S. M. Babcock.*

The officers for the ensuing year are: *president*, B. D. HALSTED; *vice president*, R. A. HARPER; *treasurer*, C. A. HOLLICK; *secretary*, G. F. ATKINSON; *councillors*, C. E. BESSEY, F. V. COVILLE.

An important step was taken by the society in appointing a committee to consider the best means of realizing the purposes of the society in "the advancement of botanical knowledge." Among other things this committee will consider the uses to which the accumulating funds of the society may be put. The committee will report at the next annual meeting of the society. —GEORGE F. ATKINSON, *Secretary.*